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Quelle influence des symbioses mycorhiziennes et des traits racinaires sur l'érosion des sols tropicaux ?

Application à la restauration écologique des écosystèmes forestiers dégradés de Nouvelle-Calédonie sur Ferralsols développés sur substrats ultramafiques

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A mes parents qui m'ont donné le goût du travail et appris à être curieux.

Ի հիշատակ Կիրակոսի եւ Արշալուսի

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Résumé « grand public »

Les forêts tropicales couvrent près de la moitié de la superficie forestière mondiale et sont l'objet de déforestation et de dégradation. Leur restauration apparaît comme un enjeu fondamental au bien-être humain. La Nouvelle-Calédonie ne fait pas exception à cette tendance et fait partie des points chauds de la biodiversité mondiale. L'objectif appliqué de cette thèse est ainsi de contribuer à la restauration écologique des forêts de l'archipel afin de limiter l'érosion des sols sur substrats ultramafiques. Nous nous focalisons, *via* une approche multi-échelle et pluridisciplinaire, sur l'influence des associations plantes - champignons (symbioses) et des racines sur l'érosion des Ferralsols développés sur ces substrats. Notre travail suggère l'existence d'un seuil limitant la restauration, permet de caractériser des espèces-outils limitant l'érosion et amène à esquisser de nouvelles pistes de recherche en vue de la restauration écologique des milieux forestiers de Nouvelle-Calédonie.

Short abstract

Tropical forests cover almost half of the world's forested area and are subject to deforestation and degradation. Their restoration appears to be a fundamental issue for human well-being. New Caledonia is no exception to this trend and is one of the hotspots of global biodiversity. Therefore, the objective of this thesis is to contribute to the ecological restoration of the archipelago's forests in order to limit soil erosion on ultramafic substrates. We focus, *via* a multi-scale and multidisciplinary approach, on the influence of plant-fungi associations (symbiosis) and roots on the erosion of Ferralsols grown on these substrates. Our work suggests that there is a threshold limiting restoration, allows to characterize tool species limiting erosion and leads to sketch new research tracks with a view to the ecological restoration of the forests of New Caledonia.

Résumé

Les écosystèmes forestiers tropicaux représentent près de la moitié de la superficie forestière mondiale. Ces écosystèmes qui fournissent des services fondamentaux pour le bien-être de nos sociétés (*e.g.* régulation des flux de matières, maintien des sols) sont particulièrement touchés (perte et dégradation des forêts) par les changements globaux. La Nouvelle-Calédonie, et ses substrats ultramafiques, ne font pas exception à cette tendance. L'activité minière et les feux sont responsables de la régression, de la fragmentation, de la dégradation des forêts et de l'érosion des sols. L'archipel est classé parmi les points chauds de la biodiversité mondiale et la restauration écologique de ces écosystèmes revêt de forts enjeux.

L'objectif appliqué de cette thèse est de contribuer à la restauration écologique des forêts de Nouvelle-Calédonie afin de limiter l'érosion des sols sur substrats ultramafiques, et s'inscrit dans le champ disciplinaire de l'écologie de la restauration. L'objectif scientifique est d'étudier l'influence des symbioses mycorhiziennes et des traits racinaires sur l'érosion des Ferralsols développés sur substrats ultramafiques à travers une approche multi-échelle.

Dans la première partie, nous mettons en évidence les caractéristiques floristiques et structurales de communautés végétales sur substrats ultramafiques. Celles-ci laissent présager une expression accrue des traits racinaires des espèces dominantes dans les forêts monodominantes. La place centrale du feu et des cyclones dans la dynamique de succession végétale est également soulignée, tout comme celle des symbioses mycorhiziennes dans le maintien de la monodominance de *Nothofagus aequilateralis*.

Dans la deuxième partie, notre travail permet de suggérer l'existence d'un seuil biotique entre les maquis ligno-herbacés dégradés et les maquis ligno-herbacés. Les feux répétés seraient la cause principale du franchissement de ce seuil. L'augmentation de la biomasse végétale constituerait en effet le facteur-clé contribuant à accroître la stabilité des agrégats entre ces deux stades. Ainsi, la protection contre les feux, associée à la promotion des successions végétales à travers l'utilisation d'espèces potentiellement facilitatrices comme *Costularia arundinacea* pourrait constituer une stratégie efficiente pour limiter l'érosion des Ferralsols. De plus, l'influence des communautés végétales (*e.g.* composition floristique) et fongiques (*e.g.* biomasse) sur la stabilité des agrégats est clairement mise en exergue.

La troisième partie vise à évaluer la capacité d'espèces végétales, associées à des champignons mycorhiziens, à accroître la stabilité des agrégats, mais aussi à identifier les traits racinaires et les associations mycorhiziennes contribuant à cet accroissement. Dans cette partie, nous mettons en évidence que la combinaison de valeurs élevées des traits racinaires « Root Mass Density – Root Length Density – pourcentage de racines fines » est efficace pour augmenter la stabilité des agrégats. Par ailleurs, l'efficacité de cette combinaison de traits racinaires est accrue par les symbioses mycorhiziennes. Ainsi, des trois espèces végétales évaluées, *Costularia arundinacea* serait l'espèce-outil la plus efficace pour accroître la stabilité des agrégats.

Ce travail a ainsi permis de mettre en évidence l'influence des traits racinaires et des symbioses mycorhiziennes sur la stabilité des agrégats des Ferralsols sur substrats ultramafiques, que ce soit à l'échelle des espèces ou des communautés végétales. A notre connaissance, ces résultats sont les premiers acquis sur ce type de sol. Ces résultats permettent de formuler des propositions en vue de la restauration écologique des milieux forestiers de Nouvelle-Calédonie afin de limiter l'érosion des sols sur substrats ultramafiques, mais aussi d'esquisser de nouvelles pistes de recherche.

Mots-clés : stabilité des agrégats du sol ; substrats ultramafiques ; traits racinaires ; mycorhizes ; restauration écologique ; Nouvelle-Calédonie.

Abstract

Tropical forest ecosystems cover nearly half of the world's forest area. These ecosystems provide basic services for the well-being of our societies (e.g. regulation of material flows, soil preservation) are particularly affected (loss and degradation of forests) by global changes. New Caledonia, and its ultramafic substrates, is no exception to this trend. Mining and fires are responsible for forest regression, fragmentation, degradation and soil erosion. The archipelago is ranked among the hotspots of global biodiversity and the ecological restoration of these ecosystems is a major challenge.

The objective of this thesis is to contribute to the ecological restoration of the forests of New Caledonia in order to limit the erosion of soils on ultramafic substrates and is part of the disciplinary field of the ecology of restoration. The scientific objective is to study the influence of mycorrhizal symbiosis and root traits on the erosion of Ferralsols developed on ultramafic substrates through a multi-scale approach.

In the first part, we highlight the floristic and structural characteristics of plant communities on ultramafic substrates. These suggest an increased expression of the root traits of dominant species in monodominant forests. The central place of fire and cyclones in the dynamics of plant succession is also emphasized, as well as mycorrhizal symbioses in maintaining the monodominance of *Nothofagus aequilateralis*.

In the second part, our work suggests the existence of a biotic threshold between degraded ligno-herbaceous maquis and ligno-herbaceous maquis. Repeated fires would be the main cause of crossing this threshold. The increase in plant biomass would be the key factor contributing to the stability of the aggregates between these two stages. Thus, fire protection combined with the promotion of plant successions through the use of potentially facilitating species such as *Costularia arundinacea* could be an efficient strategy for limiting erosion of Ferralsols. In addition, the influence of plant (*e.g.* floristic composition) and fungal communities (*e.g.* biomass) on the stability of aggregates is clearly highlighted.

The third part aims to evaluate the ability of plant species, combined with mycorrhizal fungi, to increase the stability of aggregates, but also to identify root traits and mycorrhizal associations contributing to this increase. In this section, we demonstrate that the combination of high values for “Root Mass Density - Root Length Density – percentage of fine

roots" is effective in increasing aggregate stability. Moreover, the efficacy of this combination of root traits is enhanced by mycorrhizal symbiosis. Thus, of the three plant species evaluated, *Costularia arundinacea* would be the most effective tool species for increasing the stability of aggregates.

This work allowed us to highlight the influence of root traits and mycorrhizal symbiosis on the stability of soil aggregates on Ferralsols on ultramafic substrates, at the scale of plant communities or at the level of plant species. To our knowledge, these results are the first to be acquired on this type of soil. These results make it possible to formulate proposals for the ecological restoration of forest ecosystems in New Caledonia in order to limit soil erosion on ultramafic substrates, but also to sketch new avenues of research.

Keywords : soil aggregate stability ; ultramafic substrates ; root traits ; mycorrhiza ; ecological restoration ; New Caledonia.

Avertissement au lecteur

Le contenu de cette thèse est bilingue français/anglais. Les chapitres d'introduction générale et de discussion générale & perspectives sont rédigés en français. Les autres chapitres sont rédigés en anglais et sont constitués d'articles publiés, acceptés ou soumis dans des revues scientifiques à comité de lecture pendant la durée du travail de thèse. Néanmoins, chaque chapitre en anglais est précédé d'une introduction en français présentant les objectifs, les principaux résultats et les apports des travaux réalisés.

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Chapitre 1 – Introduction générale

1. Contexte global

1.1. La dégradation des écosystèmes forestiers tropicaux

« L'ampleur de l'apport des forêts au bien-être humain est considérable. Les forêts jouent un rôle dans la lutte contre la pauvreté rurale, assurant la sécurité alimentaire et fournissant des moyens de subsistance décents ; elles offrent des occasions prometteuses de croissance verte à moyen terme et procurent des services environnementaux vitaux à long terme, comme l'air pur et l'eau propre, la conservation de la biodiversité et l'atténuation du changement climatique. »

José Graziano da Silva, Directeur général de la FAO

Les écosystèmes forestiers tropicaux sont au cœur des concertations mondiales du fait de leurs rôles dans les équilibres climatiques, de leur contribution à la biodiversité et de la place qu'ils tiennent dans la vie des populations. Ces forêts couvrent 1,7 à 2,1 milliards d'hectares selon les estimations, soit près de la moitié de la superficie forestière mondiale (Fig.1) (Mille and Louppe 2015).

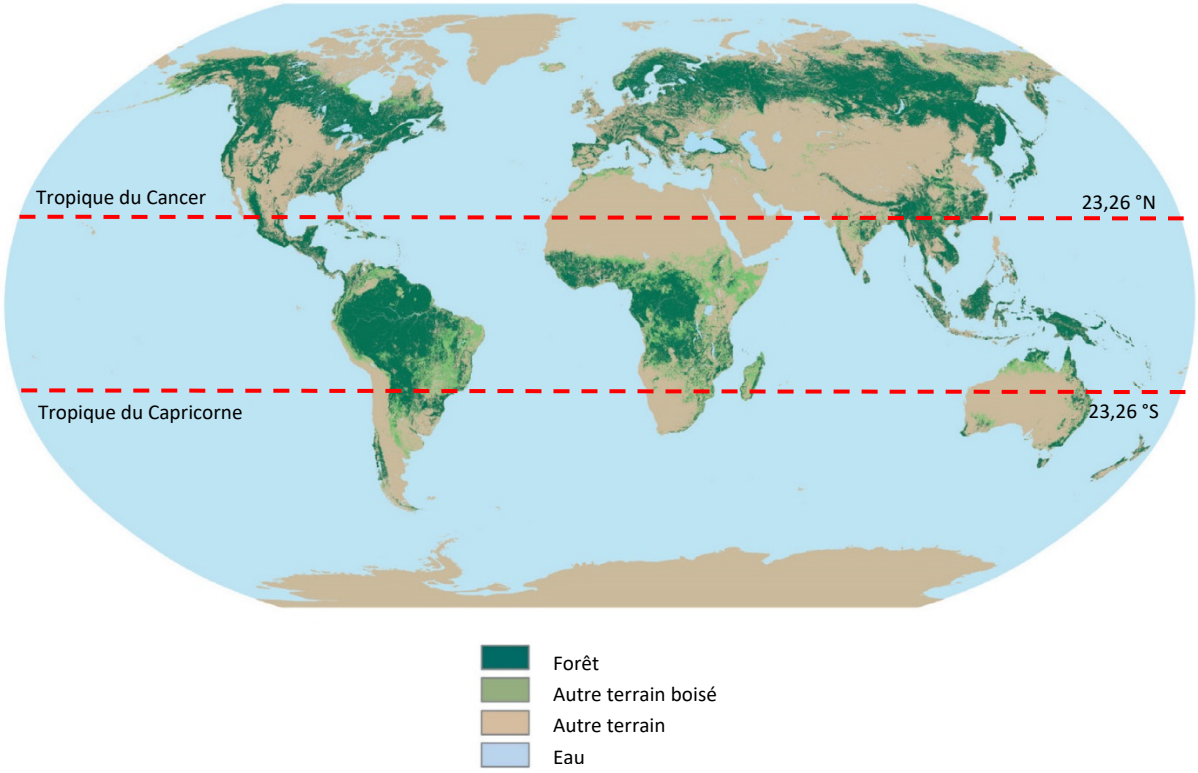

Figure 1 – Répartition mondiale des forêts

La région intertropicale abritant les écosystèmes forestiers tropicaux se situe entre les Tropiques du Cancer et du Capricorne (adapté de FAO (2005))

Si les changements climatiques à long terme devraient avoir un impact important sur l'extension et sur la composition des écosystèmes forestiers, ce sont en premier lieu les activités humaines qui ont le plus affecté les forêts mondiales depuis le 20ème siècle (Mille and Louppe 2015). Selon les données de la FAO (FAO 2016), le bilan de la période 2005-2015 fait état d'une perte annuelle brute de 8,8 millions d'hectares de forêt dont près de la moitié se concentre dans les régions tropicales. A ces surfaces s'ajoutent celles des forêts dégradées (perte de couvert, de densité, d'essences de valeur et de biodiversité) qui représenteraient plus de 2 millions d'hectares annuels en forêts denses humides. Sur la même période, les dynamiques de reforestation naturelle ou de plantation ont annuellement couvert 2 millions d'hectares et ne compensent donc pas la perte annuelle brute (Fig.2). Nous assistons ainsi à une diminution des surfaces forestières tropicales, à une dégradation de ces écosystèmes forestiers naturels et à leur remplacement partiel par de la forêt de plantation.

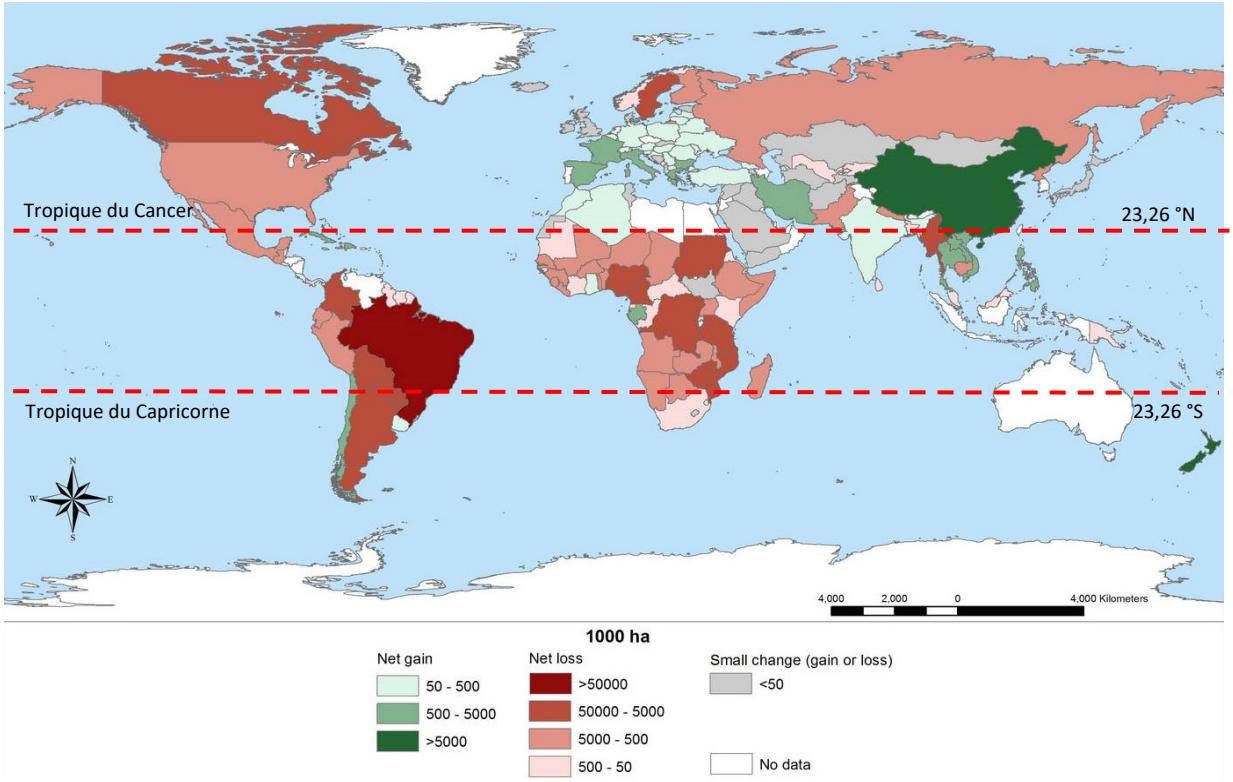

Figure 2 – Evolution des surfaces forestières en régénération naturelle entre 1990 et 2015 (adapté de FAO (2016))

Dans ce contexte, la gestion durable des écosystèmes forestiers tropicaux et leur restauration écologique apparaissent comme des enjeux fondamentaux au bien-être des populations humaines.

1.2. Qu'entend-on par restauration écologique ?

Restaurer, v. t. (lat. restaurare) : réparer, remettre en bon état

Définition du Littré

Avant d'aller plus loin, il est nécessaire de définir le terme de « restauration écologique ». Si sa création reviendrait à Aldo Leopold dans la première moitié du 20ème siècle (Zedler 1999), ce n'est qu'en 1989 que la restauration écologique a été définie par la Society for Ecological Restoration comme « le processus qui assiste l'autoréparation d'un écosystème qui a été dégradé, endommagé ou détruit ». Il s'agit de placer l'écosystème sur une trajectoire le conduisant à ressembler, par la composition et la structure de sa communauté biotique, à un « écosystème de référence » (Fig.3.). Celui-ci peut être aussi bien ce que fut l'un des stades antérieurs du milieu, qu'un stade alternatif susceptible de mieux correspondre au contexte paysager et aux capacités de gestion de la population locale (Larrère 2014). Le choix du modèle de référence n'impose aucune norme naturelle : la restauration écologique doit prendre en compte aussi bien les contraintes et les opportunités naturelles que les contraintes, les aspirations et les opportunités humaines. Il s'agit d'anticiper les différentes trajectoires envisageables pour le milieu, de les comparer à celles que suivrait l'écosystème s'il était laissé à son évolution naturelle, enfin de demander aux acteurs sociaux concernés quel état du milieu convient le mieux à leurs désirs et à leurs possibilités d'action (Larrère 2014).

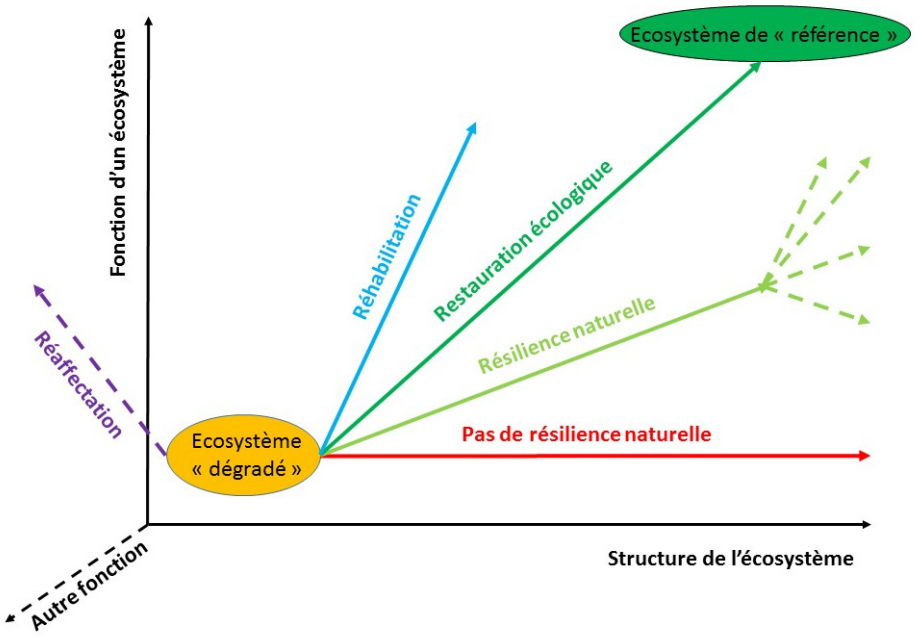

Figure 3 – Trajectoires des écosystèmes après intervention (d'après Dutoit (2014))

La restauration *sensu stricto* doit permettre d'assurer le pilotage de la structure et les fonctions de l'écosystème restauré correspondant à la trajectoire de l'écosystème de référence choisi au préalable, tandis

que la résilience naturelle peut conduire à différentes trajectoires (flèches en pointillés) en fonction de l'histoire et du contexte spatial au moment de l'arrêt de la dégradation de l'écosystème. La réhabilitation ne permet quant à elle pas d'atteindre l'ensemble de cette structure et de ses fonctions. Enfin, la réaffectation conduit à un écosystème comprenant des fonctions et une structure différentes, représentées ici dans l'espace 3D.

L'importance des moyens à mettre en œuvre pour la restauration d'un écosystème dépend largement de son niveau de dégradation, qui se traduit par des ruptures d'équilibres et le franchissement de seuils biotiques et physico-chimiques (Fig.4.).

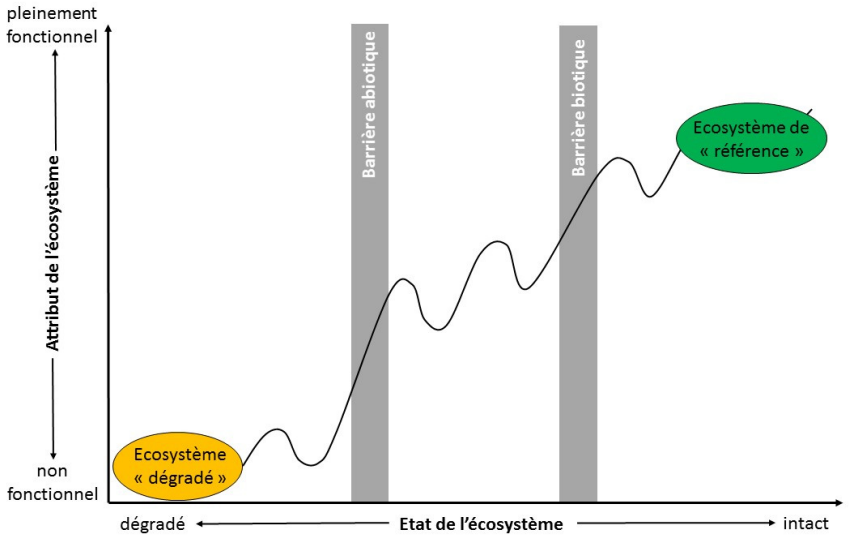

Figure 4 – Modèle conceptuel de la dégradation et de la restauration d'un écosystème (adapté de Hobbs and Harris (2001))

1.3. Les enjeux de la restauration écologique

« D'ici à 2050, la diversité biologique est valorisée, conservée, restaurée et utilisée avec sagesse, en assurant le maintien des services fournis par les écosystèmes, en maintenant la planète en bonne santé et en procurant des avantages essentiels à tous les peuples».

Plan stratégique 2011-2020 et Objectifs d'Aïchi relatifs à la Diversité Biologique

Un consensus scientifique existe quant à la perte continue d'habitats et à l'augmentation des taux d'extinction des espèces tout au long du siècle si les tendances actuelles persistent (Secrétariat de la Convention sur la diversité biologique 2010). Ces tendances font courir de graves risques aux sociétés humaines, au fur et à mesure que plusieurs seuils sont dépassés. Un grand nombre de services fournis par les écosystèmes, sous-tendus par la diversité biologique, pourraient être rapidement perdus si des

mesures urgentes ne sont pas prises pour inverser les tendances actuelles. Une meilleure protection de la diversité biologique constitue donc un investissement prudent et rentable, en termes de réduction des risques pour la communauté mondiale.

Ainsi, en octobre 2010, la conférence mondiale sur la diversité biologique a adopté un nouveau plan stratégique pour la période 2011-2020. Le fondement du plan est que la diversité biologique sous-tend le fonctionnement des écosystèmes et l'approvisionnement en services d'écosystèmes essentiels au bien-être humain. Ce plan stratégique a pour mission de « prendre des mesures efficaces et urgentes en vue de mettre un terme à l'appauvrissement de la diversité biologique, afin de s'assurer que, d'ici à 2020, les écosystèmes sont résilients et continuent de fournir des services essentiels, préservant ainsi la diversité de la vie sur Terre, et contribuant au bien-être humain et à l'élimination de la pauvreté. Pour garantir ceci, les pressions exercées sur la diversité biologique sont réduites, les écosystèmes sont restaurés, les ressources biologiques sont utilisées d'une manière durable et les avantages découlant de l'utilisation des ressources génétiques sont partagés d'une manière juste et équitable; des ressources financières suffisantes sont fournies, les capacités sont renforcées, les considérations relatives à la diversité biologique et la valeur de la diversité biologique sont intégrées, des politiques appropriées sont appliquées de manière efficace, et les processus décisionnels s'appuient sur des bases scientifiques solides et l'approche de précaution. »

Parmi les 20 objectifs du Plan stratégique 2011-2020 figure notamment, d'ici à 2020, « la restauration d'au moins 15% des écosystèmes dégradés, contribuant ainsi à l'atténuation des changements climatiques et l'adaptation à ceux-ci, ainsi qu'à la lutte contre la désertification. »

1.4. Le défi des substrats ultramafiques

« Serpentine environments are not just a fascinating and unique phenomenon in themselves but offer premier opportunities to study the origins, development, diversity, and function of life on a heterogeneous planet. »

Harrison and Rajakaruna (2011)

Les roches ultramafiques sont issues du manteau supérieur de la Terre et sont définies à partir de leur minéralogie originale composée à plus de 90 % d'olivine et de pyroxène. Si les roches ultramafiques sont relativement fréquentes au niveau des croûtes océaniques, leur présence au niveau des croûtes continentales est bien plus rare (Fig.5.) et révèle des évènements tectoniques particuliers ayant conduit à l'exposition à la surface terrestre de matériaux enfouis entre 10 et 50 km de profondeur. La majorité des substrats ultramafiques à la surface continentale sont issus d'ophiolites,

c'est-à-dire du charriage d'une portion de lithosphère océanique et de manteau supérieur sur un continent lors de la convergence de deux plaques lithosphériques (Moores 2011).

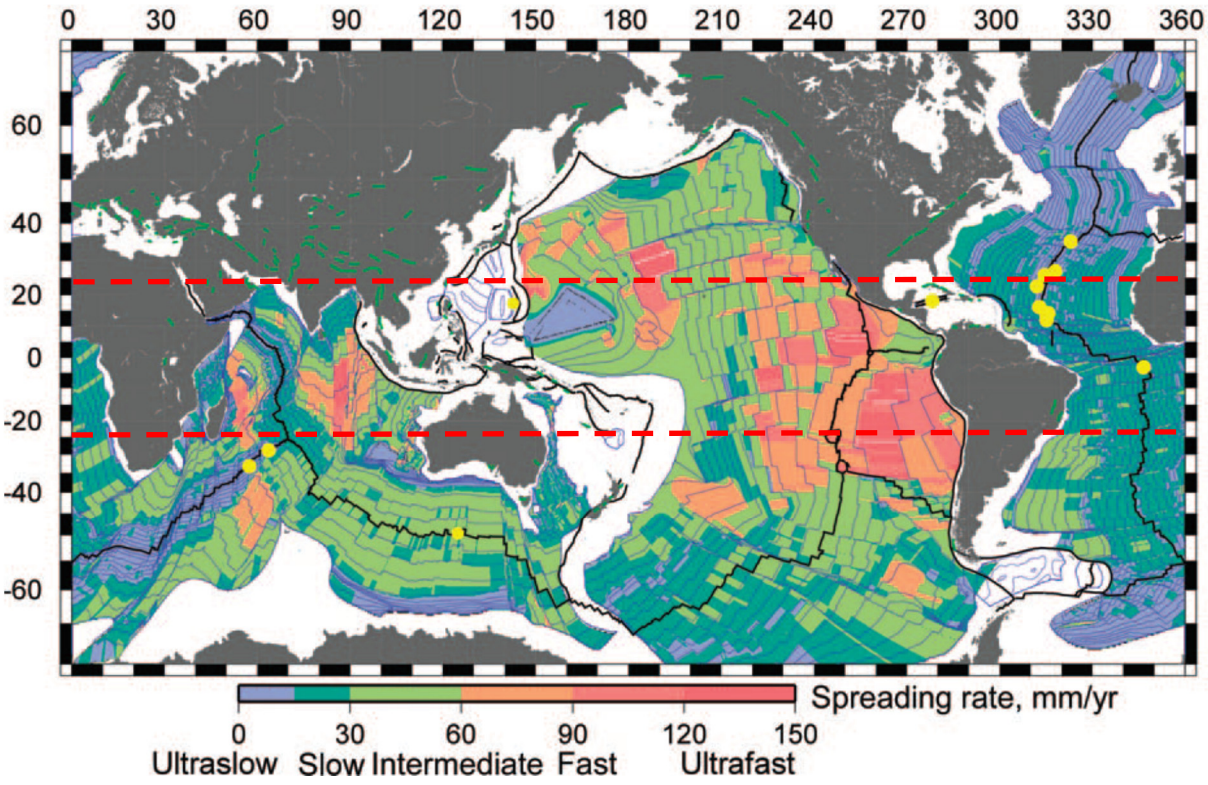

Figure 5 – Répartition des substrats ultramafiques au niveau de la lithosphère océanique et de la lithosphère continentale (d'après Guillot and Hattori (2013))

Les principales zones d'occurrence des substrats ultramafiques sont représentées en vert sur les continents et par les cercles jaunes sur les planchers océaniques. Les différentes couleurs de la lithosphère océanique correspondent à sa vitesse d'expansion. Les lignes pointillées rouge indiquent les tropiques du Cancer et du Capricorne.

En raison de leur origine géologique et de leur composition chimique unique, les substrats ultramafiques sont riches en minéraux et minerais d'intérêt commercial. Si ces substrats ne couvrent qu'environ 3 % des terres émergées (Guillot and Hattori 2013), ils font l'objet d'exploitations minières générant des perturbations conséquentes sur les écosystèmes qu'ils abritent (O'Dell and Claassen 2011). Ainsi, les latérites nickélifères, qui se développent sous climat tropical sur ce type de substrats, fournissent 30 à 40 % de la production mondiale de nickel et recèlent environ 70 % des réserves mondiales connues (Brown *et al.* 2009). La totalité du chrome mondial provient de l'exploitation de la chromite, minéral spécifique aux substrats ultramafiques (O'Dell and Claassen 2011). Les tendances de productions mondiales de ces minerais sont à l'augmentation (US Geological Survey 2016), augurant

d'un accroissement des pressions anthropiques sur les écosystèmes se développant sur substrats ultramafiques.

Cependant, la restauration écologique des écosystèmes sur substrats ultramafiques constitue un défi écologique. Les sols qui se développent sur ces substrats sont en effet contraignants pour la croissance des plantes du fait de leur déficit en éléments nutritifs – le calcium en particulier, de leur faible capacité de rétention en eau, et enfin de teneurs élevées en métaux lourds et en magnésium (Kruckeberg 1984). Par ailleurs, ces écosystèmes présentent au niveau de leur flore une diversité et des taux d'endémisme remarquablement élevés, ainsi que des relations plantes-habitats uniques (Boyd *et al.* 2004; Brooks 1987; Harrison and Rajakaruna 2011). Par exemple, en Californie, 215 taxons sont uniquement inféodés aux substrats ultramafiques (Anacker 2011). En Nouvelle-Calédonie, le taux d'endémisme des espèces végétales sur ces sols atteint 82 % (L'Huillier *et al.* 2010).

Au-delà de ce défi pour la restauration écologique, les substrats ultramafiques, du fait des contraintes édaphiques qu'ils engendrent et de leur distribution géographique « quasi-insulaire » (van der Ent *et al.* 2015), sont considérés comme un système modèle pour l'étude de l'évolution, de l'écologie et de la conservation, depuis l'échelle des cellules et des organismes jusqu'à celle des processus au niveau des écosystèmes (Harrison and Rajakaruna 2011). Ils revêtent donc un intérêt scientifique tout particulier en écologie de la restauration et ce d'autant plus lorsqu'il s'agit de la plus grande ophiolite au monde d'un seul tenant (environ 5 500 km^2), comme c'est le cas de la Nouvelle-Calédonie (Guillot and Hattori 2013).

2. La Nouvelle-Calédonie comme modèle d'étude

2.1. Un point chaud mondial de biodiversité

La Nouvelle-Calédonie est un archipel situé dans le sud-ouest de l'océan Pacifique, à 1 500 km à l'est de l'Australie et 1 900 km au nord de la Nouvelle-Zélande (Fig.6.). D'une superficie de 19 100 km^2, il s'étend sur environ 500 km de long et 50 km de large entre le 18ème et le 23ème degré de latitude sud et entre le 163ème et le 168ème degré de longitude est (Fig.6.). Il est constitué d'une île principale, la Grande Terre, prolongée au nord par les îles de Bélep et au sud par l'île des Pins, ainsi que des îles Loyauté à l'est, et de nombreux îlots et récifs inhabités (Fig.6.).

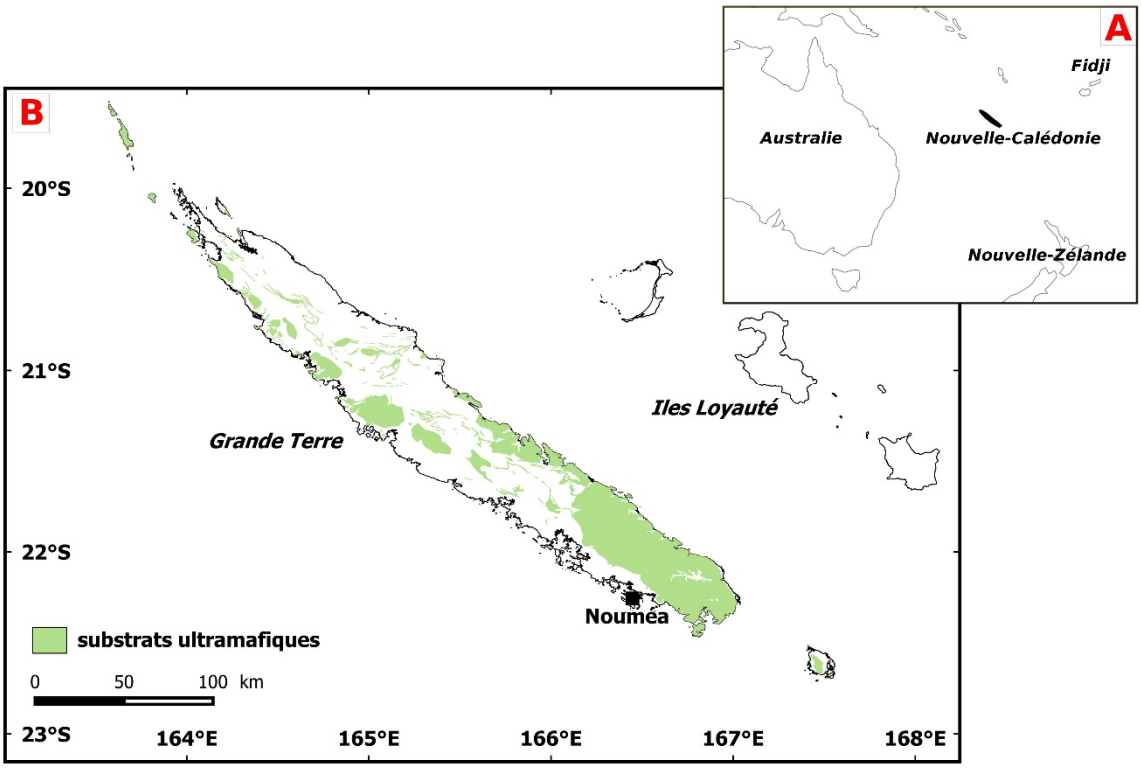

Figure 6 – Situation de la Nouvelle-Calédonie dans le sud-ouest de l'océan Pacifique (A) et répartition des substrats ultramafiques en Nouvelle-Calédonie (B)

L'archipel fait partie des dix premiers « points chauds » de biodiversité ou « hotspot » – zones présentant à la fois de fortes concentrations en espèces, des taux d'endémisme et des degrés de menace exceptionnels (Myers (1988), prioritaires pour la conservation de la biodiversité terrestre. Cette liste de zones prioritaires a depuis été élargie à 34 zones (Mittermeier *et al.* 2004). La flore calédonienne compte environ 3 370 espèces dont 74 % sont endémiques (Morat *et al.* 2012). Cette richesse floristique est attribuée à la combinaison de son isolement géographique et de la diversité climatique, géologique et topographique de l'archipel (Isnard *et al.* 2016).

Bien que les substrats ultramafiques couvrent moins d'un tiers de la superficie de la Nouvelle-Calédonie (Fig.6.), ils recèlent une fraction disproportionnellement élevée de la flore totale. Ainsi, les espèces strictement inféodées à ces substrats représentent environ 50 % de la flore endémique et présentent un taux d'endémisme très élevé (96,7 %) et supérieur à celui de la flore strictement inféodée aux substrats non ultramafiques (Isnard *et al.* 2016). Si l'endémisme édaphique est considéré comme un facteur-clé favorisant la diversité des plantes et l'endémisme dans d'autres « hotspots » de biodiversité (*e.g.* Californie, bassin méditerranéen), une compréhension holistique de la diversité et de l'endémisme de la végétation de Nouvelle-Calédonie fait encore défaut à ce jour (Isnard *et al.* 2016), rendant d'autant plus pertinentes les approches pluridisciplinaires.

Dans le même temps, les teneurs élevées en nickel des substrats ultramafiques sont à l'origine d'une exploitation minière ayant débuté il y a plus d'un siècle et qui, dans les prochaines années, risque de s'accroître sensiblement (L'Huillier *et al.* 2010). L'exploitation minière intensive, couplée aux feux dévastateurs, entraîne une dégradation importante de l'environnement terrestre en détruisant et fragmentant les formations végétales, et en mettant à nu les sols, entraînant une érosion hydrique intense. En 2007, 20 000 hectares de sols nus dégradés étaient dus à l'activité minière sur le territoire (L'Huillier *et al.* 2010).

2.2. De la revégétalisation à la restauration écologique en Nouvelle-Calédonie : un défi

Afin de réduire les impacts environnementaux de l'exploitation minière en Nouvelle-Calédonie, des actions de revégétalisation visant à remettre en place un couvert végétal, et ainsi limiter l'érosion des sols, ont été développées depuis les années 1970 (Jaffré and Pelletier 1992; Sarrailh 2001). En parallèle, des moyens techniques de gestion des déchets (stockage des stériles) et des écoulements d'eaux ont été mis en place. Au cours de ces quarante dernières années, les méthodes et pratiques de revégétalisation ont largement évolué pour s'inscrire depuis le début des années 2000 dans une démarche de restauration écologique. Cette évolution résulte en partie d'une meilleure appréhension des traits d'histoire de vie de certaines espèces de plantes locales (*e.g.* dormance des graines, adaptations particulières), ainsi que de la volonté d'accroître la résilience des milieux restaurés.

Toutefois, la restauration écologique en Nouvelle-Calédonie nécessite de faire face aux contraintes suivantes, faisant de celle-ci un véritable défi :

- les modifications profondes des conditions du milieu par l'exploitation minière mécanisée (*e.g.* décapage, déblaiement) faisant franchir des barrières biotiques et abiotiques (cf. Fig.4.) ;

- les carences en éléments nutritifs (phosphore, potassium et calcium) pour les plantes des sols sur substrats ultramafiques et *a contrario* les teneurs excessives en magnésium (L'Huillier *et al.* 2010), d'où un rapport Ca/Mg faible et des vitesses de croissance des végétaux très lentes (Mc Coy et *al.* 1999) ;
- la présence de métaux biodisponibles (nickel, manganèse, chrome, cobalt) potentiellement toxiques pour les plantes (L'Huillier *et al.* 2010) ;
- l'hétérogénéité importante des conditions environnementales (*e.g.* pédologie, altitude, exposition) (L'Huillier *et al.* 2010) ;
- la grande diversité floristique, le fort taux d'endémisme et le micro-endémisme spécifique à la Nouvelle-Calédonie (Wulff *et al.* 2013).

Pour relever ce défi de la restauration écologique, les travaux de recherche en écologie microbienne des sols sur substrats ultramafiques de Nouvelle-Calédonie se sont développés ces dernières années. De par leurs caractéristiques fonctionnelles, les champignons pourraient jouer un rôle clé dans la restauration des sols dégradés (Quoreshi 2008). L'objectif est d'optimiser l'utilisation des micro-organismes dans les processus de restauration écologique des sites miniers (Jourand *et al.* 2013; L'Huillier *et al.* 2010) afin de contribuer à lever les barrières biotiques.

Si l'ambition initiale de la revégétalisation dans les années 1970 était de limiter l'érosion hydrique afin de préserver les milieux terrestres et aquatiques, cet enjeu reste prépondérant pour la restauration écologique. Il est en effet aujourd'hui reconnu par les opérateurs miniers que l'existence sur les massifs miniers d'une couverture végétale pérenne à prédominance forestière offre le meilleur rempart aux menaces de pollution des cours d'eau, des plaines en contrebas, vouées à l'agriculture et à l'élevage, et du lagon inscrit au patrimoine mondial de l'Unesco (L'Huillier *et al.* 2010).

2.3. Les causes et les enjeux de l'érosion hydrique

Avec son relief montagneux, ses nombreuses et fortes pentes, ses précipitations élevées – jusqu'à 5 000 mm au voisinage des sommets les plus élevés – et leur caractère extrême lors de dépressions cycloniques – 634 mm en 24h enregistré lors du cyclone Gyan en décembre 1981, les sols de la Grande Terre de l'archipel sont susceptibles d'être facilement érodés (Dugain 1953). L'action de l'homme n'a fait que favoriser et accélérer les phénomènes d'érosion. La déforestation, du fait de l'exploitation forestière non durable du passé, de la prospection et de l'exploitation minière, et les feux répétés sont les deux agents à l'origine des modifications désastreuses subies par la végétation, les sols et l'hydrologie de la Nouvelle-Calédonie (Dugain 1953). Au-delà des écosystèmes terrestres, l'érosion

hydrique est considérée comme la cause la plus importante de dégradation du lagon et des récifs coralliens de l'archipel (Dumas *et al.* 2010).

Si l'érosion hydrique superficielle dépend directement de la pluviosité et de la pente, elle est influencée par la nature du sol et sa couverture. Aussi, pour conclure cette présentation synthétique de la Nouvelle-Calédonie, intéressons-nous à ses sols développés sur substrats ultramafiques et à ses diverses formations végétales.

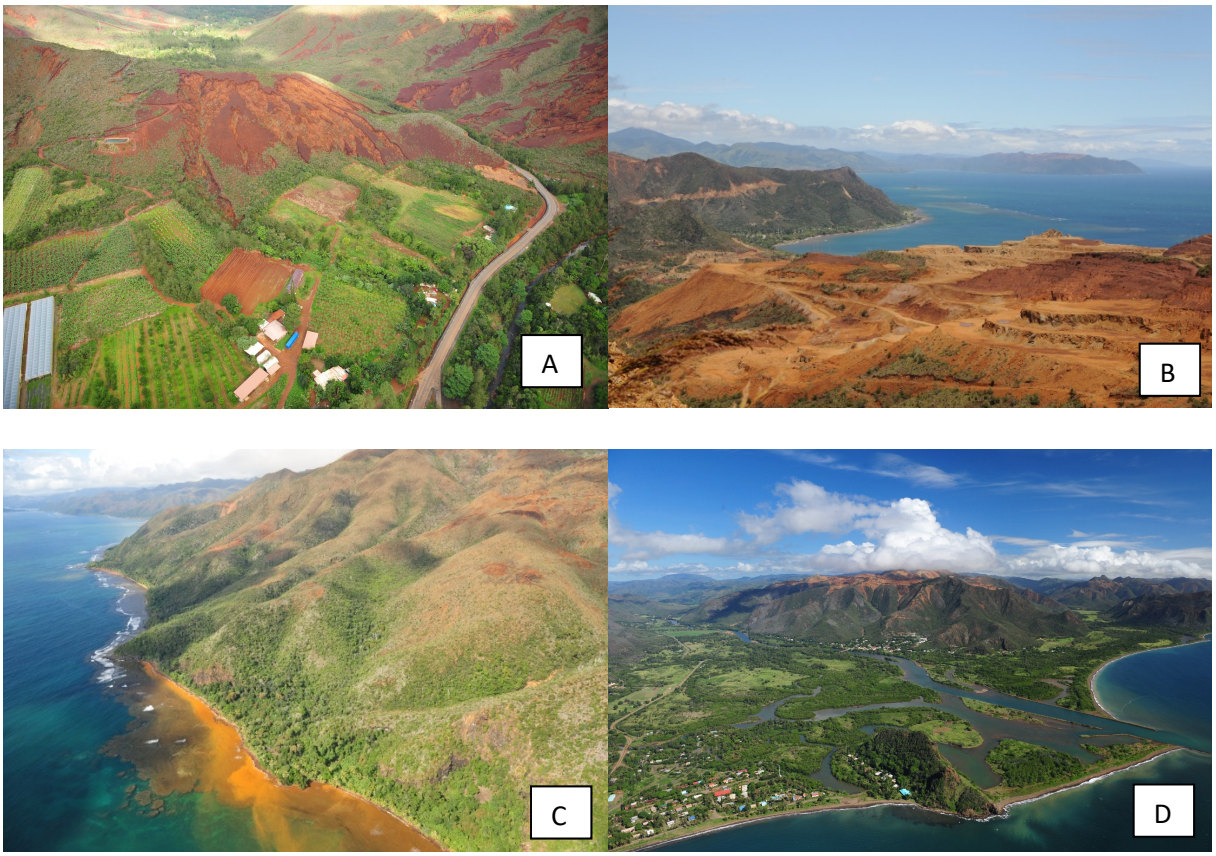

Figure 7 – Illustrations des enjeux liés à l'érosion hydrique en Nouvelle-Calédonie (photos : province Sud)
A : enjeux agricoles liés à l'érosion naturelle – col de Mouirange ; B : enjeux environnementaux liés à l'exploitation minière – mine de Thio ; C : enjeux environnementaux pour les écosystèmes marins – Côte Oubliée ; D : enjeux humains en lien avec l'activité minière – village de Thio

2.4. Les principales caractéristiques des sols sur substrats ultramafiques

Les sols de la Nouvelle-Calédonie sont issus de l'altération de roches très variées qui ont généré des exportations importantes de Na, K, Mg, Ca, plus limitées de Si. Cette altération et ces exportations entraînent une accumulation résiduelle de métaux (Fe, Al, Ni, Mn, Co, Cr …) dans des phases minérales secondaires stables (Fritsch 2012). Ce schéma très général doit être modulé par l'importance des apports pluviométriques et la capacité des couvertures d'altération à exporter les éléments dissous par drainage interne. Sur les substrats ultramafiques, deux grands types de sol sont présents, des Ferralsols et des Cambisols (Fritsch 2012).

Les Ferralsols – ou latérites (Fig.8.) - occupent essentiellement les positions hautes (*e.g.* plateau, haut de versant) des paysages et sont souvent considérés comme des sols climaciques (Fritsch 2012). Ce sont des sols minéraux de coloration rouge à brun jaune. Si les latérites sont généralement dominées par des argiles de type kaolinite, les Ferralsols sur substrats ultramafiques se distinguent par l'absence de ces argiles du fait des faibles teneurs en aluminium, au profit du magnésium. Ils se caractérisent aussi par de fortes teneurs en sesquioxydes et des oxydes de fer (hématite et goethite) (FAO 2014; Fritsch 2012). Sur l'archipel, les mécanismes de dissolution-recristallisation ont généré des sols gravillonnaires à nodules et blocs cuirassés ferrugineux. Ils sont également à l'origine de la mise en place de cuirasses ferrugineuses massives ou aujourd'hui démantelées. Cette catégorie de sols est la plus commune en Nouvelle-Calédonie sur les massifs de roches ultramafiques. Ils ont été classés comme ferrallitiques ferritiques par Latham (1975). Ils sont caractéristiques de milieux bien drainés, propices à l'exportation de la totalité des bases et d'une quantité variable de silice. Leur épaisseur peut aller de moins d'un mètre sur pente à plusieurs dizaines de mètres en zone plane.

En résumé, les Ferralsols se caractérisent principalement par (Association Française pour l'Etude du Sol 2009; L'Huillier *et al.* 2010) :

- la faible présence d'argiles de type 1:1 (essentiellement kaolinite) du fait de l'absence d'aluminium ;
- *a contrario*, la présence d'argiles granulométriques due aux oxydes de fer (oxydes > 60 % de la fraction < 2 µm) ;
- des teneurs élevées en oxydes de fer (> 30 % des oxydes totaux) ;
- des teneurs élevés en nickel, chrome et cobalt ;
- des pH fortement à moyennement acides dans les horizons supérieurs ;
- une capacité d'échange cationique faible.

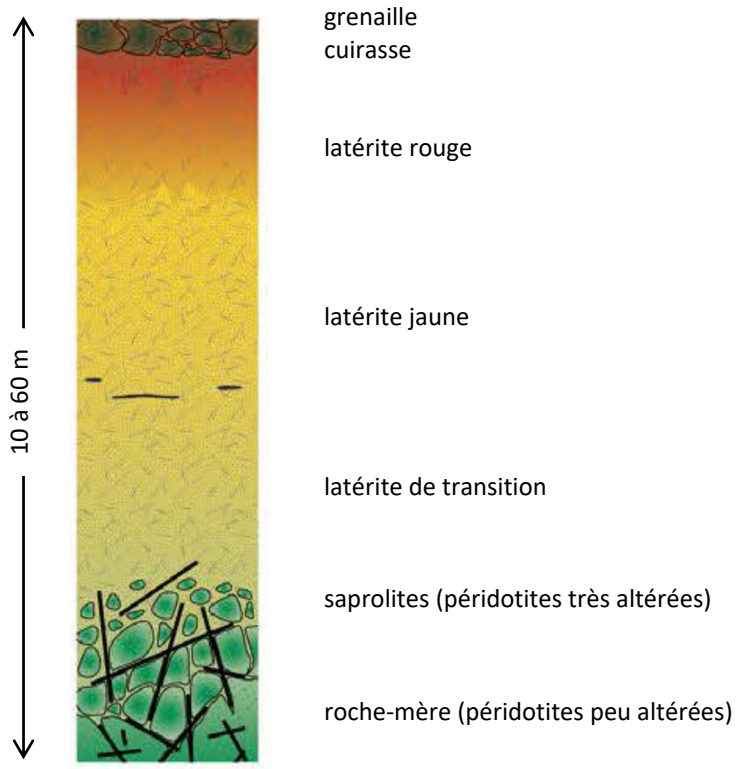

Figure 8 – Profil type de sol issu de roches ultramafiques (d'après Sevin (2014))

A l'échelon du paysage, les sols ferrallitiques ferritiques présentent des faciès très influencés par l'histoire géomorphologique du massif ultramafique et par leur position topographique actuelle. L'altération intense des silicates et des hydrosilicates concentrée dans le réseau de fracturation de la roche-mère (péridotites) favorise le développement de karsts en profondeur et de latérites vers la surface. Cette fonte géochimique est à l'origine de matériaux très poreux au niveau des karsts profonds, liquéfiables, susceptibles de générer des effondrements de terrain. Sur les pentes, elle favorise les incisions en griffes lors de glissements de terrain et de mise en charge de nappes (Fritsch 2012). Ainsi, les sols de crêtes et de pentes sont des sols érodés, rajeunis par troncature du profil initial. Ils sont en général peu profonds, parsemés de blocs rocheux et sont recouverts de manière inégale de colluvions ferrallitiques (L'Huillier *et al.* 2010).

Les Cambisols - ou sols bruns tropicaux - ont un développement vertical limité par l'érosion superficielle (Fritsch 2012). Ces sols bruns s'observent sur les flancs et à la base des massifs de péridotites et forment des sols bruns hypermagnésiens. Ils sont variablement imprégnés par la matière organique et comprennent des minéraux hérités des substrats rocheux ainsi que des minéraux néoformés, principalement des argiles (smectite, kaolinite) et des oxydes (hématite, goethite et

gibbsite). Ils couvrent des paysages ondulés ou faiblement accidentés (Fritsch 2012). Ils sont généralement peu épais et caillouteux, de couleur brune (L'Huillier *et al.* 2010).

En résumé, les Cambisols se caractérisent principalement par (L'Huillier *et al.* 2010) :

- leur richesse en argiles magnésiennes et ferrifères de type smectite (argile de type 2:1) ;
- une texture argileuse ;
- des teneurs variables en nickel et en manganèse ;
- un pH faiblement acide à basique ;
- une forte capacité d'échange cationique, du fait de la présence d'argile, saturée en majorité par Mg^{2+}.

Les fortes contraintes de ces conditions édaphiques sur substrats ultramafiques sont à l'origine de mécanismes d'adaptation des plantes. Ainsi, les associations plantes–microorganismes (*e.g.* symbioses mycorhiziennes) permettraient de mobiliser les très faibles quantités de phosphore disponible pour les plantes dans ces sols, de faciliter l'alimentation en azote chez certaines espèces végétales par des associations symbiotiques (*e.g.* symbioses à Frankia chez les Casuarinaceae) ou encore de contribuer à la tolérance de certaines plantes aux métaux naturellement présents dans les sols sur substrats ultramafiques (L'Huillier *et al.* 2010).

2.5. Les principales formations végétales sur substrats ultramafiques

La Nouvelle-Calédonie est caractérisée par la variété de ses formations végétales, la richesse et l'originalité de sa flore. La nature et la distribution des formations végétales sont liées aux conditions climatiques, au substrat, à l'altitude et aux effets de l'activité humaine.

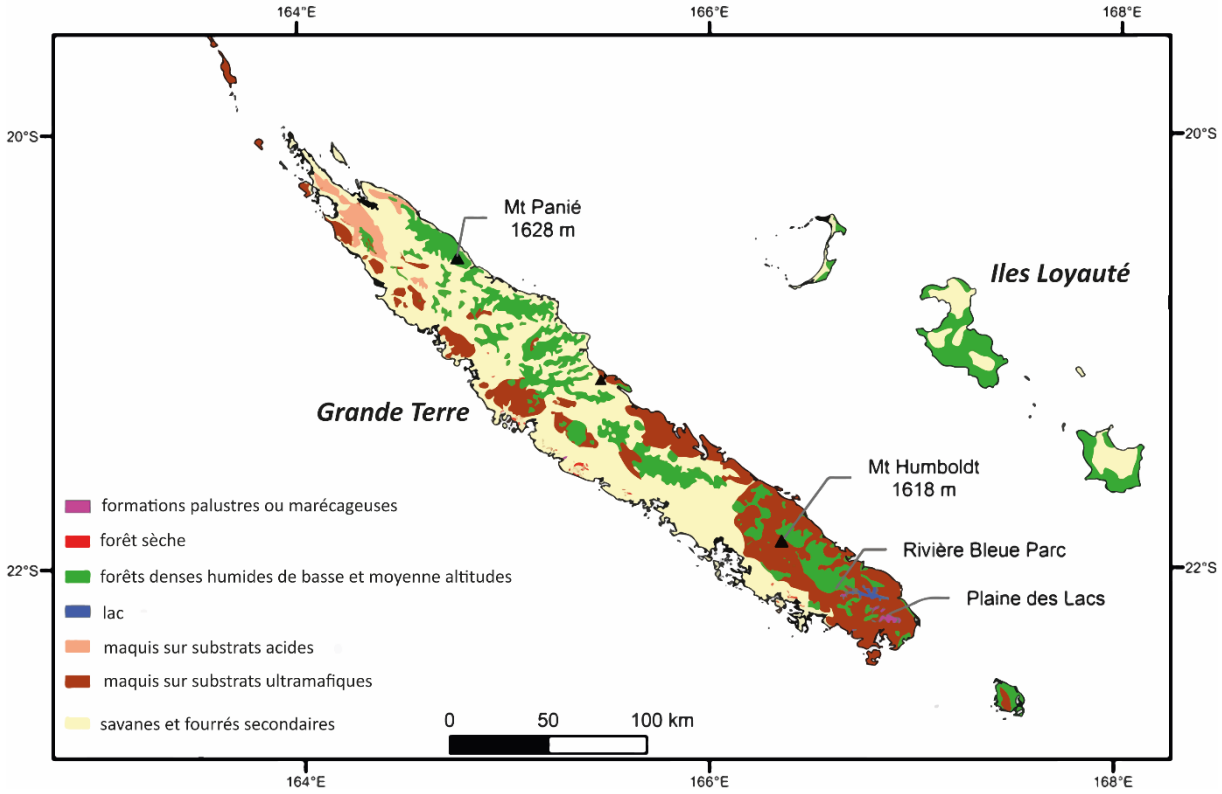

Figure 9 – Carte des principales formations végétales en Nouvelle-Calédonie (d'après Isnard *et al*. 2016)

Ainsi sur substrats ultramafiques, les formations végétales suivantes se rencontrent (Fig.9.) (Jaffré *et al.* 2012) :

- les forêts denses humides de basse et moyenne altitudes ;
- les forêts denses humides et les maquis d'altitude ;
- les maquis ;
- les formations palustres ou marécageuses.

De manière générale, les forêts denses humides sont les formations végétales les plus complexes et les plus diversifiées de l'archipel (L'Huillier *et al.* 2010). Sur substrats ultramafiques, elles rassemblent environ 1 380 espèces de plantes vasculaires dont 82 % sont endémiques (Jaffré *et al.* 2009). Elles se développent dans des zones recevant en moyenne 1 500 à 5 000 mm de pluie par an. Cette formation végétale constituait très vraisemblablement avant l'arrivée de l'homme sur l'archipel, il y a 3 500 à 4 000 ans, la formation végétale la plus répandue sur les massifs ultramafiques (L'Huillier *et al.* 2010). Ces forêts ont fortement reculé sous l'action des incendies répétés d'origine anthropique, mais aussi de l'activité minière (L'Huillier *et al.* 2010). Elles couvrent aujourd'hui environ 20 % de la superficie des substrats ultramafiques, soit 1 100 à 1 200 km^2 (Isnard *et al.* 2016).

Les forêts denses humides de basse et moyenne altitudes se rencontrent jusqu'à 900 – 1000 m d'altitude sur la Grande Terre. Ce sont celles dont l'étendue a le plus fortement régressé et qui font actuellement partie des écosystèmes les plus menacés de Nouvelle-Calédonie (L'Huillier *et al.* 2010). Outre la diminution des surfaces, ces forêts sont aujourd'hui extrêmement fragmentées. Du fait de ces dégradations, elles ne subsistent le plus souvent qu'au-dessus de 500 m d'altitude sur des sommets et des flancs de montagne. En dessous de 500 m, elles couvrent rarement des versants entiers, restant localisées aux talwegs et hauts de versants, dont les sols ferrallitiques plus ou moins érodés ou colluvionnés sont souvent recouverts d'éboulis rocheux. Dans ces forêts, la strate arborescente a une hauteur moyenne de 15 à 25 m, le diamètre des troncs ne dépassant généralement pas le mètre. Sur substrats ultramafiques, ces forêts se distinguent par la forte abondance des espèces d'Araucariaceae, de Myrtaceae, d'Apocynaceae, de Nothofagaceae et de Casuarinaceae. La dominance de certaines de ces espèces arborées permet de différencier des faciès particuliers : forêts de *Nothofagus*, forêts de Chêne gomme (*Arillastrum gummiferum*), forêts surcimées par des *Araucaria* ou encore de Casuarinaceae (Jaffré *et al.* 2012). Le sous-bois des forêts denses humides de basse et moyenne altitudes est généralement riche en palmiers et Pandanaceae. La strate herbacée y est généralement peu développée (< 10 % en couvert) et composée de Cyperaceae et de Poaceae (Isnard *et al.* 2016).

Les forêts denses humides et les maquis d'altitude se développent le plus souvent au-dessus de 900 à 1 000 m, dans des zones recevant des précipitations généralement supérieures à 3 500 mm par an. Les forêts sont basses (8 à 15 m de hauteur), fréquemment surcimées par des espèces du genre *Araucaria* (L'Huillier *et al.* 2010). La strate arborescente y est souvent constituée d'un petit nombre d'espèces appartenant aux genres *Cunonia*, *Quintinia*, *Metrosideros*, *Paracryphia* et *Weinmannia* (Jaffré *et al.* 2012). Le sous-bois est dense et caractérisé par l'abondance des fougères et des *Freycinetia* lianescents. Les branches et les troncs des arbres portent de nombreux épiphytes. Le passage d'une forêt d'altitude à un maquis se fait souvent de manière imperceptible (L'Huillier *et al.* 2010). Les maquis d'altitude se caractérisent toutefois par leur hauteur (5-6 m) et le caractère presque exclusivement héliophile de leur flore (Jaffré *et al.* 2012). Les forêts et maquis d'altitude occupent moins de 350 km^2 et possèdent une flore très originale avec de nombreuses espèces à distribution restreinte (Jaffré *et al.* 2012)

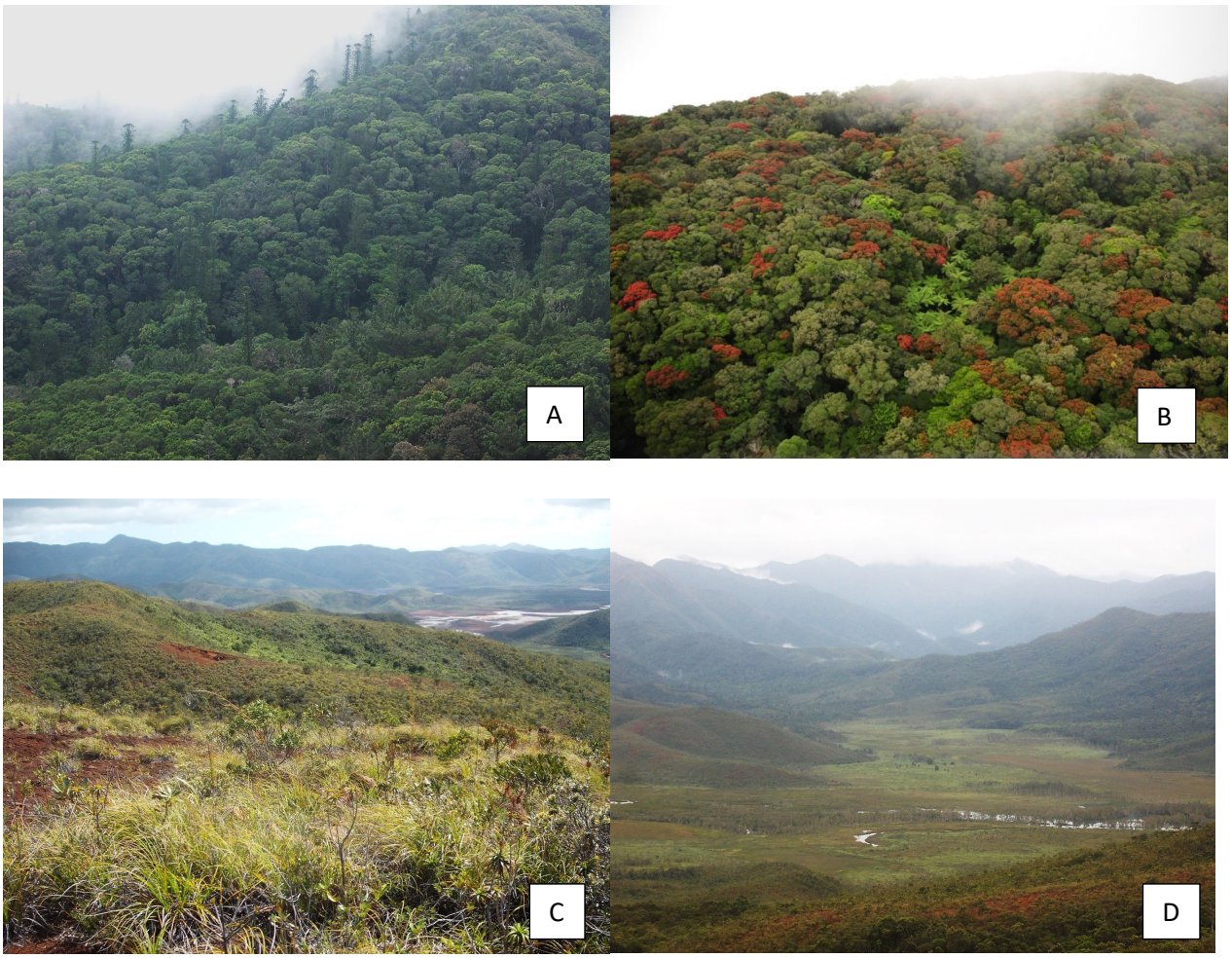

Figure 10 – Illustrations des différentes formations végétales et paysages sur substrats ultramafiques en Nouvelle-Calédonie

A : forêt dense humide de basse et moyenne altitudes – parc provincial de la Rivière Bleue (photo : J. Demenois) ; B : forêt dense humide d'altitude – pic Ningua (photo : province Sud) ; C : maquis ligno-herbacé – parc provincial de la Rivière Bleue (photo : J. Demenois) ; D : paysage de formation marécageuse – parc provincial de la Rivière Bleue (photo : J. Demenois)

Les maquis regroupent un ensemble de groupements végétaux à strate dominante inférieure à 5-6 m, sclérophylles, sempervirents et héliophiles. Ils présentent une grande variété physionomique structurale et floristique et possèdent de nombreuses formes de transition avec la forêt. La grande majorité d'entre eux résulte de la destruction de la forêt par des incendies répétés et représentent des stades variés de la succession secondaire post-incendie (L'Huillier *et al.* 2010). Les substrats ultramafiques sont aujourd'hui couverts à plus de 80 % par des maquis, soit une surface de 4 500 km^2 (Isnard *et al.* 2016). Ils rassemblent environ 1 140 espèces de plantes vasculaires, dont le taux d'endémisme est de 89 %. Les familles les plus caractéristiques de ces maquis sont, par ordre décroissant d'espèces, les Myrtaceae (> 130 espèces), les Euphorbiaceae (environ 100 espèces) puis

les Rubiaceae, Apocynaceae, Cunoniaceae, Rutaceae (> 50 espèces). Certaines familles (*e.g.* Ericaceae, Casuarinaceae), moins abondantes en espèces, sont très caractéristiques des maquis en raison de la très forte proportion de leurs espèces inféodées aux maquis (L'Huillier *et al.* 2010). La strate herbacée est constituée principalement de Cyperaceae, la famille *des* Poaceae étant très faiblement représentée et restreinte aux maquis ligno-herbacés sur sols bruns hypermagnésiens (Isnard *et al.* 2016).

Les maquis sont classés sur une base physionomique et pédologique en 4 grands groupements (L'Huillier *et al.* 2010) :

- les maquis arbustifs, à strate herbacée réduite, sur sols bruns hypermagnésiens ;
- les maquis ligno-herbacés sur sols ferrallitiques remaniés par érosion ou colluvionnement ;
- les maquis arbustifs à buissonnants sur sols ferrallitiques gravillonnaires ou cuirassés ;
- les maquis paraforestiers et préforestiers.

Les maquis ligno-herbacés sur sols ferrallitiques sont les plus communs et ont, à la même altitude, une composition floristique relativement homogène sur l'ensemble des substrats ultramafiques. Ces maquis résultent de l'impact des feux répétés et se sont largement étendus au détriment de la forêt depuis l'arrivée de l'homme (L'Huillier *et al.* 2010).

Les formations palustres ou marécageuses sont principalement représentées dans l'extrême sud de la Grande Terre sur environ 250 km^2 (L'Huillier *et al.* 2010). Elles peuvent être assimilées à du maquis ligno-herbacé des zones humides. Ce sont des groupements végétaux très spécialisés dont toutes les espèces sont adaptées aux conditions hydromorphes du sol et certaines à des périodes de submersion. La strate herbacée est constituée de Cyperaceae. Ces formations renferment des espèces à distribution restreinte.

3. Objectifs et démarche scientifique

3.1. Objectif appliqué et cadre scientifique général

L'objectif appliqué de ce travail de thèse est de contribuer à la restauration écologique des milieux forestiers de Nouvelle-Calédonie afin de limiter l'érosion des sols sur substrats ultramafiques. Ce travail s'inscrit naturellement dans le champ disciplinaire de l'écologie de la restauration.

Comme le souligne Dutoit (2014), un meilleur pilotage des écosystèmes, et donc de leur restauration écologique, ne sera possible qu'à partir de l'acquisition de plus de connaissances écologiques sur le fonctionnement et les impacts de certains organismes vivants (considérés *a priori* comme facilitants) sur la dynamique et l'orientation des trajectoires successionnelles. Sur substrats ultramafiques, le rôle fonctionnel des symbioses mycorhiziennes au sein des formations végétales serait fondamental et permettrait de faire face aux conditions édaphiques extrêmes (Alexander *et al.* 2007; Branco 2010; Schechter and Bruns 2008). Ainsi, la plupart des plantes seraient en associations symbiotiques avec des endomycorhizes (AMF) ou des ectomycorhizes (ECM). Celles-ci faciliteraient la nutrition de la plante notamment en augmentant l'assimilation du phosphore, mais aussi en diminuant la toxicité potentielle pour les plantes induite par la présence naturelle de métaux lourds (*e.g.* Ni, Cr) dans les sols sur substrats ultramafiques (Jourand *et al.* 2014; Smith and Read 2010). Toutefois, on estime actuellement que seulement 2 % des espèces de champignons ont été inventoriés en Nouvelle-Calédonie (Jourand *et al.* 2013). Aussi, l'apport des connaissances sur les symbioses mycorhiziennes en Nouvelle-Calédonie pour la restauration écologique des écosystèmes dégradés semble-t-il majeur et beaucoup reste à faire au niveau scientifique. C'est pourquoi, ce travail de thèse s'attache à aborder conjointement les organismes végétaux et les organismes fongiques afin d'explorer leurs interactions fonctionnelles et *in fine* de contribuer à mieux utiliser les associations plantes – microorganismes dans les processus de restauration écologique.

La démarche mise en œuvre repose sur une approche multi-échelle (Fig. 11). A l'échelle des communautés, elle consiste à s'appuyer sur l'étude du fonctionnement des écosystèmes forestiers afin de caractériser la trajectoire successionnelle naturelle depuis un écosystème dégradé vers un écosystème de référence. L'enjeu est de parvenir à identifier les barrières abiotiques et biotiques (Fig. 4) afin de définir les potentiels moyens d'intervention en restauration écologique pour franchir ces seuils.

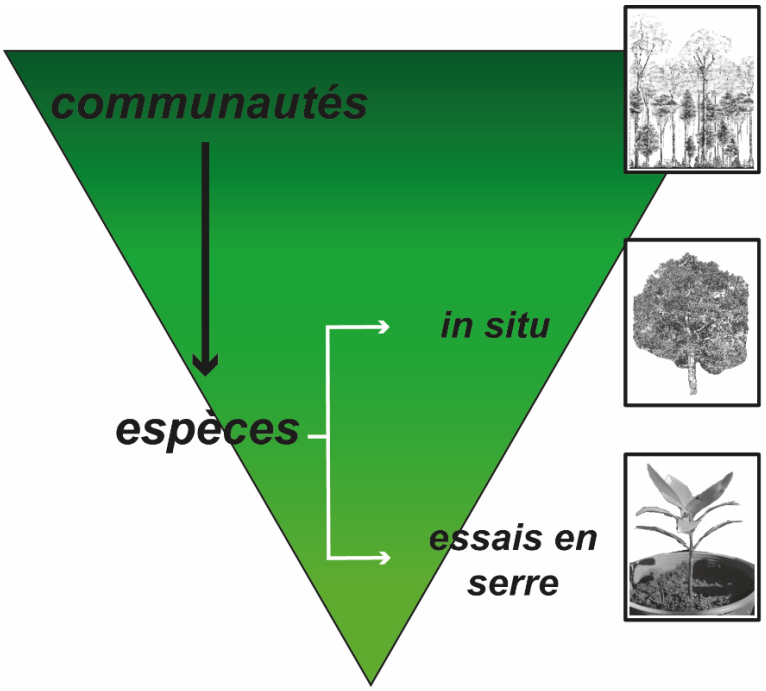

Figure 11 – Représentation schématique de l'approche multi-échelle mise en œuvre

Pour ce faire, notre travail s'intéresse à des communautés végétales caractéristiques du Sud de la Grande Terre sur sols ferralitiques ferritiques correspondant à une succession végétale potentielle ou à différents états alternatifs (Suding *et al.* 2004) : maquis ligno-herbacé dégradé par les feux à répétition > maquis ligno-herbacé à *Tristaniopsis glauca* > forêt dense humide de basse et moyenne altitude monodominante à *Arillastrum gummiferum* > forêt dense humide de basse et moyenne altitude monodominante à *Nothofagus aequilateralis* > forêt dense humide de basse et moyenne altitude (Fig. 12). Le choix de retenir des formations végétales comportant des espèces végétales dominantes (*T. glauca*, *A. gummiferum*, *N. aequilateralis*) se justifie par le fait que celles-ci contribuent significativement à la structuration des communautés de microorganismes en général, et à celle des ECM en particulier (Gourmelon 2016). En se focalisant sur ces formations et ces espèces, nous faisons donc l'hypothèse que ces espèces végétales dominantes pourraient jouer un rôle clé dans le fonctionnement des écosystèmes forestiers et donc dans leur restauration écologique.

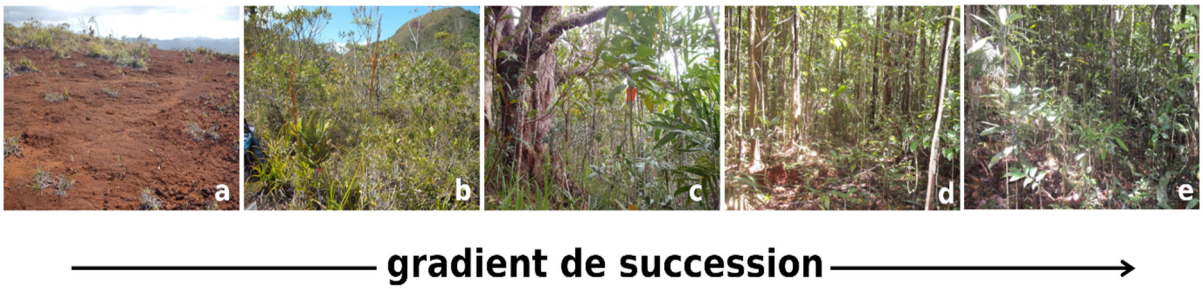

Figure 12 – Trajectoire successionnelle hypothétique étudiée sur sols ferrallitiques ferritiques

a : maquis ligno-herbacé dégradé par les feux à répétition ; b : maquis ligno-herbacé à *Tristaniopsis glauca* ; c : forêt monodominante à *Arillastrum gummiferum* ; d : forêt monodominante à *Nothofagus aequilateralis* ; e : forêt dense humide de basse et moyenne altitude (photos : J. Demenois)

L'approche à l'échelle des communautés est complétée d'une approche à l'échelle espèce, centrée sur trois espèces végétales dominantes connues pour être en association avec des champignons mycorhiziens : *Costularia arundinacea* (Sol. Ex Vahl) Kük. (Cyperaceae), *Tristaniopsis glauca* Brongn. & Gris (Myrtaceae) et *Arillastrum gummiferum* (Pancher ex Brongn. & Gris) Baill. (Myrtaceae) (Fig. 13). Ce focus à l'échelle espèce vise à approfondir les connaissances sur les interactions fonctionnelles entre plantes et champignons à travers leur étude en milieu naturel (*in situ*) et en conditions contrôlées (essais en serre). Par ailleurs, dans une optique de restauration écologique, une telle approche nous semble en adéquation avec les pratiques actuelles de revégétalisation en Nouvelle-Calédonie et les « possibilités d'action » (Larrère 2014) des opérateurs de la restauration écologique. En effet, ces trois espèces héliophiles sont couramment utilisées dans les opérations de restauration écologique sur les substrats ultramafiques de l'archipel.

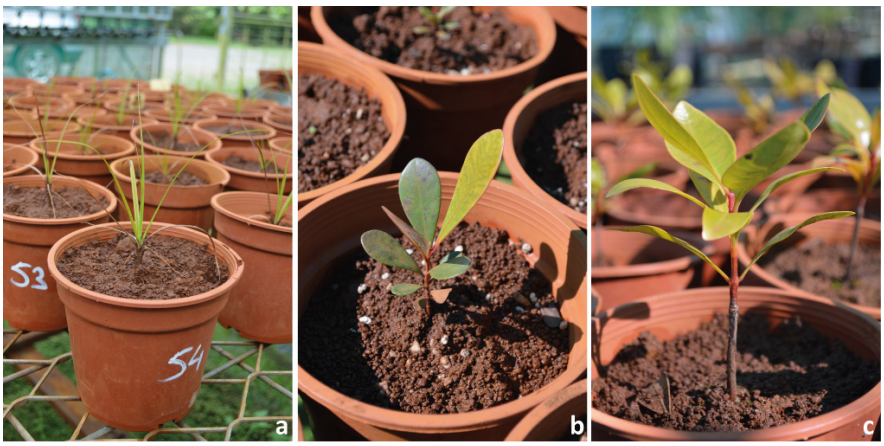

Figure 13 – Les trois espèces-modèles étudiées

a : *Costularia arundinacea* (Cyperaceae) ; b : *Tristaniopsis glauca* (Myrtaceae) ; c : *Arillastrum gummiferum* (Myrtaceae) (photos : J. Demenois)

Les actions de revégétalisation en Nouvelle-Calédonie ont été initialement menées pour limiter l'érosion hydrique sur les sols mis à nu et ont évolué à présent vers la restauration écologique des milieux naturels. La couverture végétale limite en effet l'érosion hydrique superficielle, et ce d'autant plus que cette couverture est dense et pluristratifiée (Vennetier *et al.* 2014) :

- le feuillage intercepte une partie de la pluie. Il réduit ainsi l'énergie cinétique des gouttes qui atteignent le sol indirectement, et donc leur impact érosif direct ;
- les herbes, la litière et les racines superficielles ralentissent la mobilisation des particules de sol par ruissellement ;
- les racines charpentières plus profondes des arbres limitent indirectement l'érosion en s'opposant aux glissements superficiels et en partie au tassement du sol ;
- la structure des couches humifères du sol limite leur sensibilité à l'impact des gouttes de pluie et à l'entraînement des particules de sol. De même, une forte porosité favorise l'infiltration de l'eau ;
- les débris de végétaux morts gisant au sol jouent aussi un rôle de protection, et la répartition spatiale de la végétation ou de ces débris compte autant que le pourcentage de surface qu'ils couvrent.

En revanche, bien que les racines soient considérées comme jouant un rôle essentiel dans le contrôle de l'érosion, la recherche quantitative consacrée à l'importance de l'atténuation de l'érosion hydrique par les racines est relativement limitée, principalement du fait de difficultés méthodologiques (Reubens *et al.* 2007). Par ailleurs, les racines jouent un rôle essentiel dans l'écologie des plantes (*e.g.* croissance, santé) et ce d'autant plus qu'elles sont le siège des associations plantes – champignons. Ainsi, ce travail de thèse se focalise sur les racines, les symbioses mycorhiziennes et sur leur influence sur l'érosion hydrique superficielle des sols ferrallitique ferritiques, ceux-ci n'ayant à ce jour pas fait l'objet de recherche en Nouvelle-Calédonie.

Afin d'étudier cette influence des racines et des symbioses mycorhiziennes sur l'érosion des sols ferrallitiques ferritiques, nous avons choisi de nous intéresser à la stabilité des agrégats du sol. En effet, de celle-ci dépend fortement l'érosion hydrique du sol (Barthès and Roose 2002). Par ailleurs, la stabilité des agrégats est notamment influencée par les racines et les champignons (Tisdall and Oades 1982). Aussi, l'étude de la stabilité des agrégats apparaît comme particulièrement pertinente pour étudier les interactions entre érosion, racines et symbioses mycorhiziennes.

L'objectif appliqué initial est ainsi reformulé en l'objectif scientifique suivant : ***évaluer l'influence des racines et des symbioses mycorhiziennes sur la stabilité des agrégats des Ferralsols sur substrats ultramafiques afin d'optimiser la restauration écologique des écosystèmes forestiers dégradés de Nouvelle-Calédonie.***

Cet objectif se décline en deux questions scientifiques principales prenant en compte l'approche multi-échelle :

- ***quelle est l'influence des traits racinaires des communautés végétales et des symbioses mycorhiziennes sur la stabilité des agrégats des Ferralsols sur substrats ultramafiques ?***
- ***des communautés aux espèces végétales, quelles espèces-outils potentielles pour accroître la stabilité des agrégats des Ferralsols sur substrats ultramafiques ?***

Par ailleurs, une meilleure caractérisation de la trajectoire successionnelle naturelle entre les trois formations forestières étudiées s'est avérée préalablement nécessaire, étant donné le peu d'études réalisées sur les forêts monodominantes à *Arillastrum gummiferum* et le déficit de connaissances sur l'écologie de cette espèce. Ainsi, les deux questions scientifiques principales ont été complétées par les questions suivantes :

- ***quelles sont les caractéristiques structurales et floristiques des formations forestières étudiées ?***
- ***quelles sont les stratégies écologiques conduisant à la monodominance d'Arillastrum gummiferum et de Nothofagus aequilateralis ?***

L'organisation du présent manuscrit (Fig. 14) reprend ces différentes questions scientifiques, en partant de l'approche à l'échelle des communautés pour aborder ensuite l'échelle des espèces végétales.

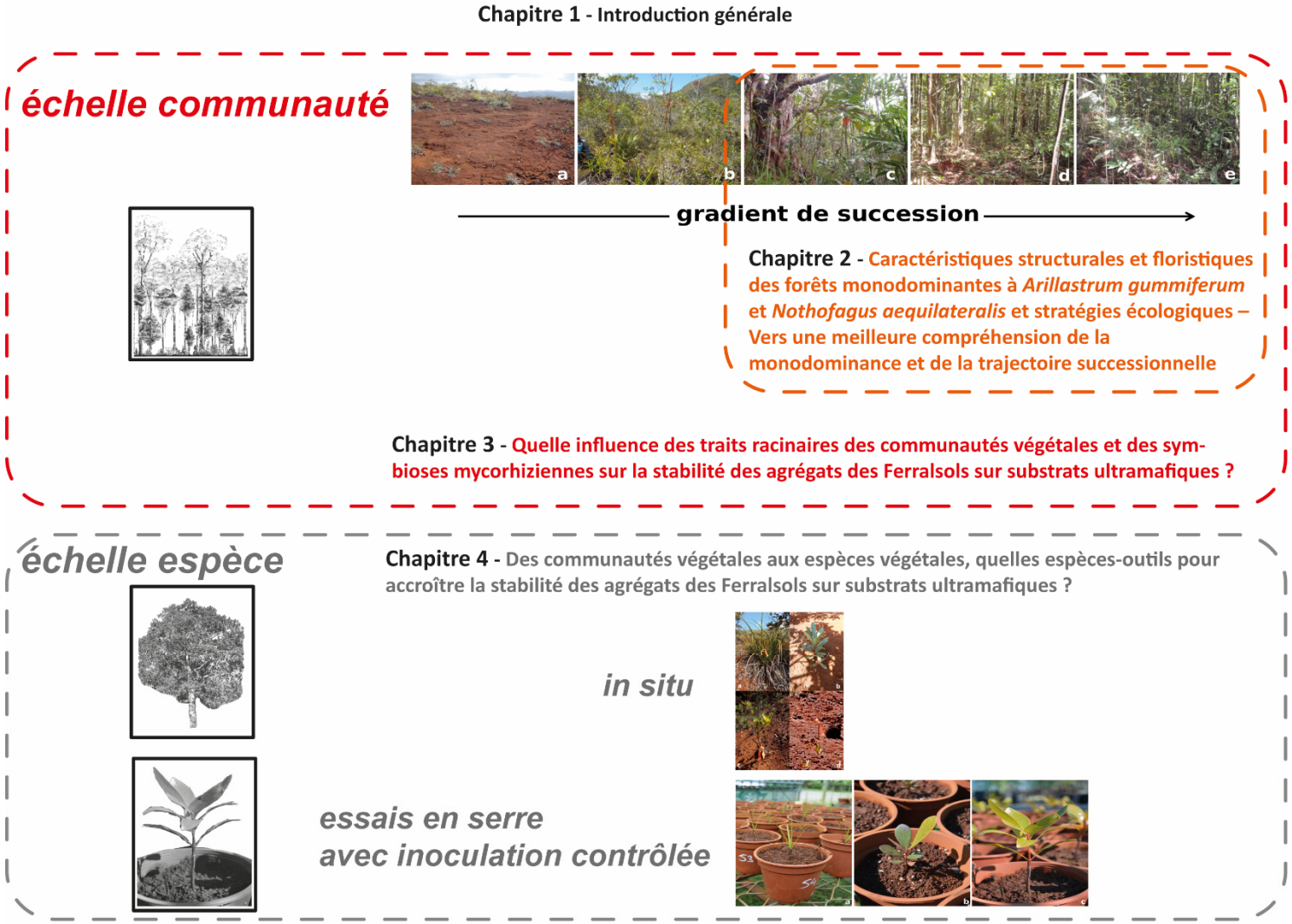

Figure 14 – Plan illustré de l'organisation du manuscrit de thèse

3.2. Objets d'études et cadre théorique

3.2.1. Une approche des racines par les traits fonctionnels

Les traits fonctionnels sont des paramètres morphologique, physiologique ou phénologique mesurables à l'échelle de l'individu, de la cellule à l'organisme entier, sans référence à l'environnement ou d'autres niveaux d'organisation, ayant une influence sur la valeur sélective des individus *via* leurs effets sur la croissance, la reproduction et la survie des individus (Violle *et al.* 2007). Ces traits fonctionnels représentent les stratégies écologiques des individus et déterminent comment les plantes répondent aux facteurs environnementaux, affectent d'autres niveaux trophiques et influencent les propriétés des écosystèmes (Pérez-Harguindeguy *et al.* 2013). Il existe de plus en plus de preuves que la variation des traits des plantes et leurs associations, à l'intérieur et entre les espèces, est associée à de nombreux processus écologiques majeurs à diverses échelles (Pérez-Harguindeguy *et al.* 2013). Leur utilisation permet de comparer un très grand nombre d'espèces et d'étudier ainsi leurs stratégies respectives. L'approche par les traits fonctionnels a donc un potentiel certain pour produire des règles généralisables à des milieux très divers (Erktan 2013). Cette approche, très répandue en écologie des communautés (McGill *et al.* 2006), présente également d'importantes potentialités en écologie de la restauration (Pywell *et al.* 2003), où le besoin de règles généralisables est également fortement présent.

L'utilisation d'une approche par les traits fonctionnels dans ce travail de thèse se justifie par les raisons suivantes :

- la diversité des communautés végétales étudiées, présentant des compositions floristiques et des structures (*e.g.* couverture végétale, stratification verticale) hétérogènes ;
- l'approche multi-échelle nécessitant de disposer de paramètres comparables à différentes échelles ;
- l'objectif d'identifier des espèces-outils sur la base de caractéristiques fonctionnelles génériques permettant les comparaisons entre espèces.

3.2.2. Une approche de la sensibilité à l'érosion par la stabilité des agrégats du sol

L'érosion du sol correspond à l'arrachement, au transport et au dépôt de particules et d'agrégats de sol (Ruellan 2010). Pour comprendre les mécanismes en jeu, il est nécessaire de s'intéresser au sol. L'Association Française pour l'Etude du Sol (2009) le définit comme un objet naturel, continu et tridimensionnel, formé de constituants minéraux et organiques, présents à l'état solide, liquide ou gazeux. Ces constituants sont organisés entre eux, créant ainsi des structures spécifiques du milieu pédologique, tels que les agrégats. Les agrégats du sol sont des regroupements de particules du sol

dans lesquels les forces qui stabilisent les particules entre elles sont plus fortes que celles entre agrégats adjacents (Martin et al. 1955). L'érosion hydrique va entraîner l'arrachement des agrégats eux-mêmes mais aussi leur désagrégation en particules. En effet, l'infiltration de l'eau et l'érosion du sol dépendent fortement de la stabilité des agrégats du sol (Bryan 1969 ; De Ploey and Poesen 1985 ; Barthès and Roose 2002).

Quatre mécanismes principaux de désagrégation peuvent être identifiés (Le Bissonnais 1996). Ces mécanismes coexistent dans les conditions du sol et leur intensité dépend des conditions du milieu :

1. l'éclatement provoqué par la compression de l'air emprisonné entre les agrégats lors de l'humectation du sol. L'intensité de l'éclatement dépend du volume d'air piégé, donc de la teneur en eau initiale des agrégats et de leur porosité (Le Bissonnais 1990).
2. la microfissuration par gonflement différentiel des argiles du sol lors des épisodes d'humectation et de dessiccation des argiles, entraînant des fissurations dans les agrégats. L'importance de ce mécanisme dépend en grande partie de la teneur en argile des sols et du type d'argiles ;
3. la désagrégation mécanique par l'impact des gouttes de pluie. Elle intervient principalement lorsque le sol est saturé en eau. L'énergie cinétique des gouttes d'eau n'est plus absorbée mais transformée en force de cisaillement ;
4. la dispersion physico-chimique due à la diminution des forces attractives entre particules colloïdales lors de l'humectation du sol (Emerson 1967). C'est le mécanisme de désagrégation le plus efficace, car il concerne les particules élémentaires et décuple les autres mécanismes (Bresson and Boiffin 1990).

Il existe de nombreuses méthodes pour évaluer la stabilité des agrégats. Quelle que soit la méthode utilisée, l'estimation de la stabilité des agrégats reste un indicateur plus qu'une mesure *stricto sensu*. Parmi ces méthodes, les tests dits de « Le Bissonnais (1996a) (repris dans la norme Afnor (2005) NF X 31-515) présentent une corrélation forte avec l'érosion (De Noni *et al.* 2002) et ont donc étaient utilisés dans notre travail.

3.2.3. Les facteurs influençant la stabilité des agrégats du sol

Si les agrégats sont formés par la combinaison de particules minérales avec des substances organiques et inorganiques, leur formation et leur stabilité sont influencées par des facteurs abiotiques et biotiques (Fig. 15).

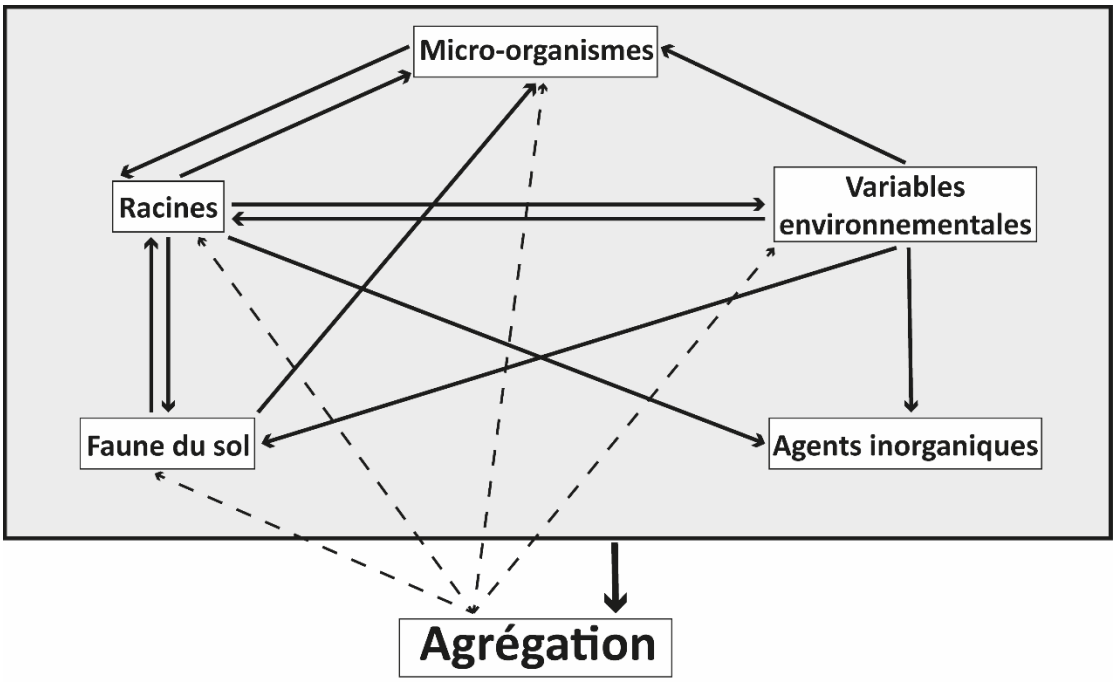

Figure 15 – La multiplicité des interactions et des rétroactions entre les 5 facteurs majeurs influençant la formation des agrégats et leur stabilisation (Six *et al.* 2004)

Au chapitre des paramètres abiotiques, les propriétés du sol suivantes influencent la stabilité des agrégats du sol (Bronick and Lal 2005; Le Bissonnais 1996a) :

- la texture du sol. La stabilité des agrégats augmente avec la teneur en argile, sans toutefois qu'il soit possible d'établir de corrélations significatives généralisables à tous les types de sols (Le Bissonnais 1996b). L'effet de la teneur en argile dépend en particulier de la teneur en eau (Gollany *et al.* 1991) ;
- la minéralogie des argiles. Le type d'argile joue un rôle ambivalent sur la stabilité des agrégats. Les argiles avec une capacité d'échange cationique forte (*e.g.* argiles de type 2 :1) induisent des agrégats plus résistants, car elles offrent une surface de contact plus importante, mais elles peuvent se disperser plus facilement quand les conditions s'y prêtent ;
- la teneur en sodium, calcium et autres cations. La nature et la teneur en cations échangeables influencent la stabilité des agrégats par leur effet sur les processus de dispersion / floculation des argiles. Cette caractéristique est fortement liée à la texture du sol et au type d'argile ;
- les oxydes de fer et d'aluminium. Ces oxydes jouent le rôle de floculant dans le sol et contribuent ainsi à augmenter la stabilité des agrégats en servant de « ponts » entre les différentes composantes de la structure. Leur effet est particulièrement effectif et observé dans les sols tropicaux, où les teneurs en argiles sont importantes (Six *et al.* 2002) ;
- la teneur en calcaire. L'apport du $CaCO_3$ a un effet favorable sur la stabilité des agrégats mais est fonction de la teneur en argile. L'effet du calcaire est principalement dû à l'ion Ca^{2+}.

Outre ces paramètres abiotiques, la matière organique du sol est un des facteurs importants de l'agrégation des particules solides dans le sol. Elle intervient à différents niveaux d'organisation de la structure, sous des formes différentes en fonction du niveau d'échelle considéré (*e.g.* racines, microorganismes, composés organiques). Tisdall and Oades (1982) proposent un modèle d'organisation hiérarchique des agrégats du sol que nous utiliserons comme cadre théorique dans la suite de notre travail. Ce modèle (Fig. 16) décrit différents types de matières organiques en fonction de leur effet stabilisant et de leur échelle :

- des agents transitoires (*e.g.* polysaccharides) qui peuvent être décomposés rapidement par les micro-organismes du sol ;
- des agents temporaires (*e.g.* racines, filaments fongiques) ;
- des agents persistants (*e.g.* composés humiques associés à des cations métalliques (Fe^{3+}, Al^{3+}).

Dans ce modèle, les agents persistants sont associés à la cohésion des micro-agrégats (< 250 µm). Les agents transitoires et temporaires permettraient de regrouper ces micro-agrégats pour former des macro-agrégats (> 250 µm) (Fig. 16). Compte tenu du type de liaison des structures entre elles, la stabilité des micro-agrégats est considérée comme très forte. *A contrario*, les macro-agrégats sont plus sensibles à la désagrégation et peuvent être désagrégés par des contraintes physiques comme les pluies. De plus, la stabilité des macro-agrégats influe sur l'ensemble des facteurs et des conditions physiques relatifs à la germination des plantes (Richard and Boiffin 1990) et à leur enracinement (Tardieu 1990).

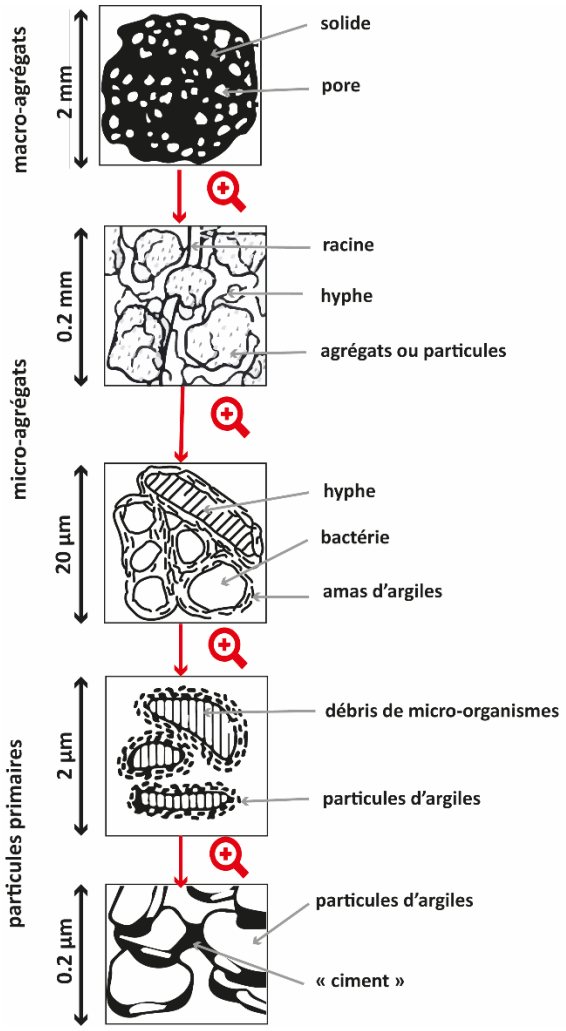

Figure 16 – Modèle d'organisation d'un agrégat avec les principaux agents stabilisants (Tisdall and Oades 1982)

3.2.4. L'influence des racines et des symbioses mycorhiziennes sur la stabilité des agrégats des sols ferrallitiques

Sur les sols ferrallitiques, les cations métalliques polyvalents (Fe^{3+}, Al^{3+}), les oxydes et les hydroxydes de Fe et Al, mais aussi la matière organique du sol, les racines et les micro-organismes associés sont considérés comme les principaux facteurs d'agrégation et de stabilisation (Dalal and Bridge 1996; Oades and Waters 1991). De manière synthétique, les racines et les symbioses mycorhiziennes peuvent influencer la stabilité des agrégats du sol *via* (Degens 1997; Tisdall and Oades 1982) :

- la production ou la décomposition de composés organiques (agents transitoires) ;
- l'enchevêtrement physique des micro-agrégats et des particules du sol par les racines et les filaments fongiques (agents temporaires) ;
- l'apport de composés humiques (agents persistants).

Dans le modèle de Tisdall and Oades (1982), les racines sont considérées comme des agents de liaison temporaires. La présence de racines augmenterait la stabilité des macro-agrégats (Habib *et al.* 1990; Pojasok and Kay 1990). Leurs effets sur l'agrégation des sols, résumés par Amézketa (1999), consistent à :

- enchevêtrer et lier les particules du sol en macro-agrégats stables, et ce même si la racine est morte ;
- assécher le sol autour des racines et ainsi réorienter les argiles parallèlement à l'axe de la racine et lier les particules du sol entre elles ;
- fournir des résidus organiques décomposables dans le sol ;
- contribuer à la présence d'une abondante communauté de microorganismes dans la rhizosphère ;
- fournir de la nourriture aux animaux du sol (*e.g.* vers de terre et mésofaune) ;
- libérer des cations polyvalents et ainsi augmenter les concentrations d'ions en solution.

L'effet des racines sur la stabilité des agrégats serait globalement positif même si quelques nuances sont à apporter (Amézketa 1999). En effet, l'architecture des racines par exemple détermine l'influence globale de leur pénétration sur l'agrégation (Carter *et al.* 1994). L'exsudation des racines, et donc leurs apports en composés organiques, est fonction des espèces végétales (Haynes and Beare 1997; Hütsch *et al.* 2002). Enfin, la décomposition des racines mortes dépend de la quantité de matière et de sa facilité à être décomposée (Robinson and Jacques 1958).

Les champignons sont également des agents temporaires dans le modèle de Tisdall and Oades (1982). La stabilité des macro-agrégats serait significativement corrélées à la biomasse microbienne (Bruce *et al.* 1992; Carter 1992; Gupta and Germida 1988; Kandeler and Murer 1993; Sparling *et al.* 1992). En ce qui concerne les champignons, ceux-ci contribueraient à la stabilité des agrégats à différentes échelles spatiales directement par des mécanismes de liaisons électriques, adhésives ou d'enchevêtrement (Graf and Frei 2013). Toutefois, si l'effet positif des champignons à endomycorhizes arbusculaires (AMF) sur la stabilité des agrégats a été mis en évidence à plusieurs reprises (Martin *et al.* 2012; Miller and Jastrow 2000; Tisdall and Oades 1982), il n'en est pas de même pour les champignons ectomycorhiziens (ECM). L'influence des ECM sur la stabilité des agrégats a été suggérée (Rillig and Mummey 2006; Tisdall 1991) et Thornton *et al.* (1956) sont les premiers à avoir démontré leur rôle important dans l'agrégation. Les caractéristiques des ECM font dire à Graf and Frei (2013) que ceux-ci seraient parfaitement adaptés pour permettre l'agrégation du sol et assurer la stabilité des

agrégats, de la même manière que les racines et leurs exsudats mais à plus petite échelle. En effet, la partie des ECM assurant le contact entre le sol et la racine présente des formes plus diverses et différenciées que les autres types de mycorhizes (Garbaye 2013). La structure filamenteuse des hyphes (de quelques microns de diamètre) atteint plusieurs dizaines de centrimètres de longueur, voire plusieurs mètres, et permet aux champignons ectomycorhiziens d'explorer le sol à grande distance de la plante (Garbaye 2013). De plus, leur production de métabolites (*e.g.* polysaccharides, hydrophobines) agissant comme de la colle sur les particules du sol a été mise en évidence et irait dans le sens d'un rôle des ECM dans la formation des agrégats (Caesar-Ton That *et al.* 2001).

Outre l'effet direct des AMF et des ECM, ceux-ci influenceraient indirectement la stabilité des agrégats du sol à travers leurs relations étroites avec le système racinaire des plantes. Rillig and Mummey (2006) proposent une revue complète de ces effets indirects. De manière synthètique, les mycorhizes auraient un effet sur :

- l'enchevêtrement des particules du sol par les racines et leur force de pénétration. La morphologie et l'architecture des racines (*e.g.* niveau de ramification, diamètre des racines) sont modifiées par les ECM. Les racines à ECM ont une structure hiérarchisée tandis que la majorité des plantes ont des racines fines à structure fractale (Garbaye 2013). Ainsi, chez les plantes ECM, les racines longues s'allongent en permanence par leur extrémité en se ramifiant et portent latéralement des racines courtes qui sont le siège de la symbiose. Ces racines ne présentent pas de coiffe, leur développement est très limité, tout comme leur durée de vie (Garbaye 2013). Pour ce qui est des AMF, leurs effets sur la morphologie et l'architecture des racines seraient moins marqués bien qu'ayant été observés (Berta *et al.* 1993) ;
- le régime hydrique du sol. Un assèchement localisé du sol, à proximité des racines, favorise les liaisons entre les exsudats racinaires et les argiles (Reid and Goss 1982). Si les mycorhizes peuvent influencer la croissance des plantes et donc le régime hydrique, il a été montré que les plantes mycorhizées présentent des relations à l'eau différentes que les plantes non mycorhizées (Augé 2001; Augé 2004). Par exemple, une conductance stomatique et une transpiration plus importantes pourraient survenir sur les plantes mycorhizées (Augé *et al.* 2004; Ebel *et al.* 1997). L'exploration plus efficace de l'eau grâce aux symbioses mycorhiziennes entrainerait des cycles humidification/dessiccation plus extrêmes. De plus, les symbioses permettraient d'accroître la quantité de carbone séquestrée par les feuilles pendant les épisodes de stress hydrique (Duan *et al.* 1996). Ainsi, les apports de carbone dans le sol s'en trouveraient augmentés, ce qui serait particulièrement marqué dans les environnements arides ;

- la rhizodéposition, ou libération de composés issus des racines vivantes, peut être fortement influencée par les champignons mycorhiziens (Jones *et al.* 2004) du fait de leur impact potentiel sur le métabolisme du carbone de la plante (Douds *et al.* 2000). Au-delà des modifications quantitatives de la rhizodéposition, des changements qualitatifs peuvent aussi survenir (Jones *et al.* 2004). Les exsudats racinaires fournissent une part importante du carbone contribuant à la formation des agrégats et à leur stabilisation à court terme (Morel *et al.* 1991). De plus, le carbone rhizodéposé peut alimenter l'activité microbienne qui en retour contribue à la formation d'agrégats ;
- la décomposition des racines. Celle-ci contribue à l'agrégation *via* l'apport de matière organique. Les symbioses mycorhiziennes peuvent influencer la qualité de cette matière organique en induisant des changements dans la chimie des racines (Langley and Hungate 2003) qui pourrait influencer à la fois les taux de décomposition et la nature des produits issus de celle-ci. Les champignons ECM peuvent également influer négativement les taux de décomposition de la litière, un effet connu sous le nom « d'effet Gadgil » (Gadgil and Gadgil 1971).

Cette synthèse met en évidence la complexité des relations entre la stabilité des agrégats du sol, les racines et les symbioses mycorhiziennes.

Chapitre 2 – Caractéristiques structurales et floristiques des forêts monodominantes à *Arillastrum gummiferum* et *Nothofagus aequilateralis* et stratégies écologiques – Vers une meilleure compréhension de la monodominance et de la trajectoire successionnelle

Ce chapitre a donné lieu à un article publié dans la revue *Australian Journal of Botany* :

- Demenois J., Ibanez T., Read J., Carriconde F., 2017. *Comparison of two monodominant rain forests in New Caledonia: the cases of Arillastrum gummiferum (Myrtaceae) and Nothofagus aequilateralis (Nothofagaceae),* Australian Journal of Botany, **65**:11-21.

La finalité de ce travail était de disposer d'une meilleure compréhension des dynamiques écologiques et caractérisation de la trajectoire successionnelle naturelle entre les trois formations forestières étudiées. En effet, les successions végétales pouvant influencer la stabilité des agrégats (Cheng *et al.* 2015; Erktan *et al.* 2016; Lin *et al.* 2014; Qiu *et al.* 2015), une telle caractérisation était nécessaire avant d'étudier l'influence des traits racinaires des communautés végétales et des symbioses mycorhiziennes sur la stabilité des agrégats des Ferralsols sur substrats ultramafiques. Par ailleurs, les forêts monodominantes à *Arillastrum gummiferum* ont été peu étudiées et l'écologie de cette espèce est finalement mal connue (Read *et al.* 2015). Enfin, *Arillastrum gummiferum* et *Nothofagus aequilateralis* sont connues pour être associées à des champignons ectomycorhiziens (McCoy 1991; Papineau 1989), dont l'implication dans la monodominance est suspectée (Connell and Lowman 1989).

Les objectifs scientifiques de ce travail étaient de :

- décrire les caractéristiques structurales et floristiques des forêts monodominantes à *A. gummiferum* ;
- comparer ces caractéristiques avec celles de forêts adjacentes monodominantes à *N. aequilateralis* et de forêts denses humides de basse et moyenne altitude ;
- mieux comprendre et comparer les mécanismes impliqués dans la monodominance d'*A. gummiferum* et de *N. aequilateralis*.

Au-delà de ces objectifs, l'étude de la monodominance revêt un intérêt majeur pour la compréhension de l'écologie des forêts tropicales. En effet, les forêts tropicales humides accueillent généralement une grande diversité d'espèces végétales au niveau de leur canopée (Whitmore 1984)

et les forêts dominées par une seule espèce (ou monodominance) ont longtemps été considérées comme des anomalies écologiques (Hart 1990). Connell and Lowman (1989) ont fourni une définition large de la forêt monodominante. Il s'agit d'une forêt où une seule espèce représente au moins 50 % des espèces de la canopée, de la surface terrière, des tiges ou de la biomasse sur pied. On distingue classiquement deux types de monodominance (Hart 1990) :

- le type I où l'espèce dominante persiste au-delà d'une génération. L'espèce dominante est alors habituellement une espèce de succession tardive, peu dispersée et tolérante à l'ombre qui s'établit sans perturbations apparentes ;
- le type II qui se caractérise par une dominance non persistante où l'espèce dominante est habituellement une espèce pionnière, à longue dispersion et intolérante à l'ombre qui ne peut s'établir dans le sous-bois à moins qu'une grande perturbation ne se produise.

Un troisième type de monodominance, appelé dominance transitoire, a été récemment proposé par Newbery *et al.* (2013) afin de prendre en compte le cas d'espèces dont l'abondance fluctue au cours du temps. Dans ce cas-là, la dominance repose sur le ré-établissement *in situ* après une grande perturbation externe des espèces intolérantes à l'ombre et peu dispersées. A travers ces trois types de monodominance, on voit que les perturbations environnementales tiennent une place centrale et nous verrons par la suite (Chapitre 3) que celles-ci influent également très probablement sur la stabilité des agrégats du sol.

Les principaux résultats de ce travail sont les suivants :

- la monodominance d'*A. gummiferum* s'exprime en termes de surface terrière tandis que celle *N. aequilateralis* se caractérise par l'abondance de ses tiges ;
- la richesse spécifique et les différents indices de diversité présentent des valeurs comparables entre les forêts monodominantes et la forêt dense humide de basse et moyenne altitude, suggérant que la monodominance ne limite pas la diversité végétale ;
- *A. gummiferum* et *N. aequilateralis* contribuent de manière significative aux dissimilarités floristiques entre les trois formations forestières ;
- le type de monodominance d'*A. gummiferum* et de *N. aequilateralis* est conforme à une dominance de type transitoire ;
- la monodominance d'*A. gummiferum* serait maintenue par le passage du feu grâce à la relative résistance de l'espèce à ce type de perturbation, lui permettant de survivre et de se régénérer ;

- la monodominance de *N. aequilateralis* serait maintenue par la stratégie de soutien des adultes vers les plantules à travers le réseau mycélien, combinée au passage des cyclones ;
- la longévité d'*A. gummiferum* (> 400 ans), son caractère héliophile et sa capacité à résister à certains régimes de feu permettraient à l'espèce de coloniser lentement, depuis la lisière de ces forêts monodominantes, le maquis ligno-herbacé adjacent. Ainsi, la forêt monodominante à *A. gummiferum* serait un stade intermédiaire entre le maquis ligno-herbacé et la forêt dense humide de basse et moyenne altitude.

Ce travail a ainsi permis de préciser la trajectoire successionnelle des communautés végétales étudiées, même si la succession complète entre chacun des stades demeure hypothétique et que les différents types de forêts correspondent très probablement à différents états alternatifs (Suding *et al.* 2004). Par ailleurs, il a confirmé la place centrale occupée par les feux et les cyclones dans la dynamique de succession végétale, deux paramètres influençant la stabilité des agrégats du sol comme nous le verrons dans le chapitre suivant. Les contributions significatives d'*A. gummiferum* et de *N. aequilateralis* aux dissimilarités floristiques entre les trois formations forestières laissent présager une expression accrue des traits racinaires de ces deux espèces dans les forêts monodominantes et ce d'autant plus que l'abondance des tiges de ces espèces est élevée. Enfin, le rôle central suspecté des symbioses mycorhiziennes dans le maintien de la monodominance de *N. aequilateralis* illustre l'influence des champignons du sol sur la composition des communautés végétales. Cela justifie un peu plus la nécessité d'aborder conjointement les communautés végétales et fongiques tel que cela est fait dans le chapitre suivant, qui s'intéresse à l'influence des traits racinaires des communautés végétales et des symbioses mycorhiziennes sur la stabilité des agrégats.

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Comparison of two monodominant species in New Caledonia: floristic diversity and ecological strategies of *Arillastrum gummiferum* (Myrtaceae) and *Nothofagus aequilateralis* (Nothofagaceae) rainforests

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Abstract. Mechanisms leading to monodominance in rainforests are still commonly discussed within the framework of forest succession. Here, we focused on the comparison of two monodominant species, *Arillastrum gummiferum* (Myrtaceae) and *Nothofagus aequilateralis* (Nothofagaceae), to try to better understand the underlying ecological mechanisms. Those two species are known to dominate the upper canopy of some rainforests on ultramafic substrates in New Caledonia. We investigated the structure, diversity and composition of *Arillastrum*-dominated plots and compared them with adjacent *Nothofagus*-dominated and mixed rainforest plots. We found that the dominance of *Arillastrum* was more pronounced in terms of basal area, whereas for *Nothofagus* the dominance was mainly in terms of stem density. Species richness and diversities in the two dominated forests were not lower than those observed in mixed rainforests, suggesting that monodominance would not lead to a limitation of diversity. Finally, our observations were consistent with a transient dominance for the two species. We suggest that resistance of *Arillastrum* to some wildfire regimes would allow the species to survive and regenerate, whereas *Nothofagus* may have a supportive strategy towards their seedlings through mycorrhizal networks. Both competitive advantages would contribute to the maintenance of monodominance.

Additional keywords: ectomycorrhizal symbiosis, floristic dissimilarity, forest dynamics, mixed rainforest, transient dominance, ultramafic substratesrainforest.

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Introduction

Tropical rainforests usually host high plant species diversity (Whitmore 1984) and forests dominated by a single species (hereafter monodominance) have long been viewed as ecological anomalies (Hart 1990). A comprehensive way to understand the mechanisms leading to monodominance is to compare different cases (Fonty *et al*. 2011). Indeed, although many studies have described monodominance across the tropics, for example, *Gilbertiodendron dewevrei* (Fabaceae) in central Africa, *Shorea albida* (Dipterocarpaceae) in Asia, and *Mora excelsa* (Fabaceae) in South and Central America, few studies have attempted to analyse the mechanisms leading to monodominance throughout a comparative framework (Connell and Lowman 1989; Hart 1990; Newbery *et al*. 2013). Connell and Lowman (1989) provided a broad definition of monodominant forest, as follows: a forest where ≥50% of the canopy-tree cover, basal area, stems or biomass belongs to a single species. On the basis of the population dynamics of the species and its persistence over generations, they defined the following two major types of monodominance: Type I consists of a single-dominant species persisting beyond one generation, whereas Type II consists of a non-persistent dominance. In the Type I, the dominant species is usually a late successional, poorly dispersed and shade-tolerant species that establishes without apparent disturbances, whereas in the Type II, the dominant species is usually an early successional, long-dispersed and shade-intolerant species that cannot establish in the undergrowth unless a large disturbance occurs and opens the canopy (Hart 1990). Recently, the theoretical framework of monodominance was extended with a third type called transient dominance, to cover the case of fluctuating highly abundant species over time (Newbery *et al*. 2013). Transient dominance relies on *in situ* (re)establishment after large external disturbance of shade-intolerant and poorly dispersed species. Then, even if the

dominant canopy species cannot establish under its own shade, monodominance could appear if disturbance occurs and allow the species to regenerate in the gaps. Although these types provide a good framework to analyse and classify the different cases of monodominance, the mechanisms leading to late successional monodominant forests may be multifactorial (Peh *et al.* 2011).

In New Caledonia, a biodiversity hotspot (Myers *et al.* 2000) located in the South-West Pacific (Fig. 1), *Nothofagus aequilateralis* (Nothofagaceae) and *Arillastrum gummiferum* (Myrtaceae) commonly form monodominant forests on the main island (called *Grande Terre*; Read and Jaffré 2013). In this part of the archipelago, rainforest mainly occurs as forest patches and is surrounded by shrub-dominated vegetation (*maquis*). *Nothofagus* forests often occur as patches within or adjacent to mixed rainforest (Read *et al.* 2000). *Nothofagus aequilateralis* is endemic to New Caledonia, occurs predominantly in forests on ultramafic substrates and is ectomycorrhizal (McCoy 1991). Structure, floristic diversity and ecology of *Nothofagus* forests have been studied for more than 20 years in New Caledonia (Read and Hope 1996; Read and Jaffré 2013). These forests are characterised by the dominance of *Nothofagus* in the uppermost canopy, although *Nothofagus* does not necessarily dominate in terms of basal area or stem density (Read *et al.* 2000). Disturbances appear to be involved in the establishment and persistence of *Nothofagus* forests, at least at low or mid-elevations (Read and Jaffré 2013); therefore, this case would be an example of early successional monodominant forest.

In comparison, little is known about the ecology of *Arillastrum* forests (Read *et al.* 2015), despite the abundance of the species and its frequent logging in the 19th century (Papineau 1989). *Arillastrum* occurs in large stands (Sebert 1874) that can reach several thousand hectares (assessment by Papineau 1989) and is known to form monodominant forest (Virot 1956) adjacent to *maquis* or mixed rainforest (Papineau 1989). Jaffré (1980) classified these forests as a type of dense evergreen rainforest formation. The species is monotypic, endemic to New Caledonia and belongs to a sister lineage of the Australian eucalypt group (Ladiges and Cantrill 2007). It grows exclusively on ultramafic substrates in the south of the *Grande Terre*, with another population on the eastern coast near Houaïlou (Papineau 1989). The first records of the species mentioned its large diameter, above 2 m (Sebert 1874), and therefore its potential high longevity. Those characteristics, combined with its association with ectomycorrhizal fungi (Papineau 1989), make it of particular interest to focus on the monodominance of the species, because ectomycorrhizal fungi could contribute to it (Connell and Lowman 1989).

The aims of the present study were (1) to describe the structural and floristic characteristics of some monodominant *Arillastrum* forests, (2) to compare these with adjacent *Nothofagus* forests and mixed-canopy rainforests and, finally, (3) to understand and compare the mechanisms involved in monodominance of *Arillastrum* and *Nothofagus*.

Materials and methods

Study area

We studied the following three sites located in the south of the Grande Terre: Col de Mouirange Haut, Col de Yaté and Pic du Grand Kaori. Each site included the three studied forest types, namely mixed rainforest, *Arillastrum* and *Nothofagus* forests (Fig. 2). At each of these three sites, Read *et al.* (2000) already established one plot in the mixed rainforest and one plot in the *Nothofagus* forest. We completed this network by adding one 0.25-ha plot (50 m × 50 m) per site in the *Arillastrum* forests.

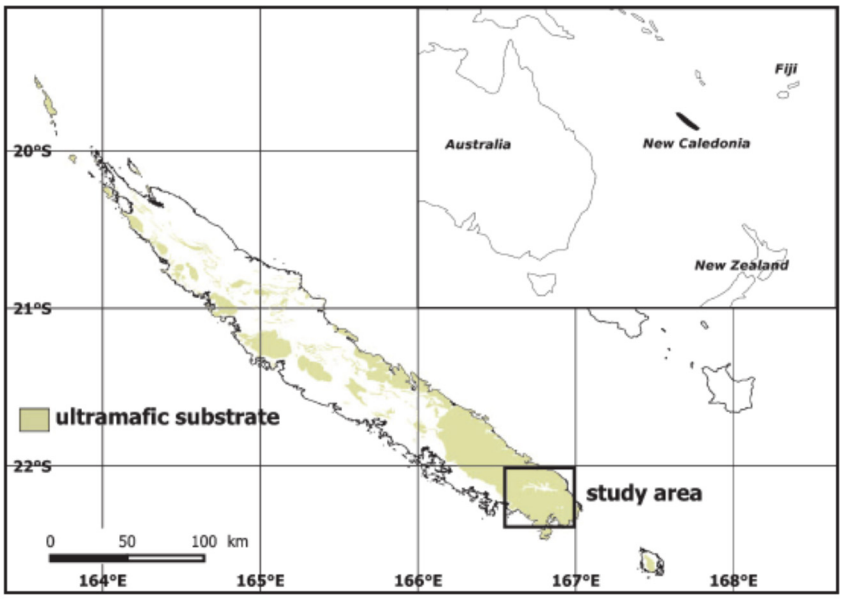

Fig. 1. Location of the study area in New Caledonia. The study area is indicated by the black square.

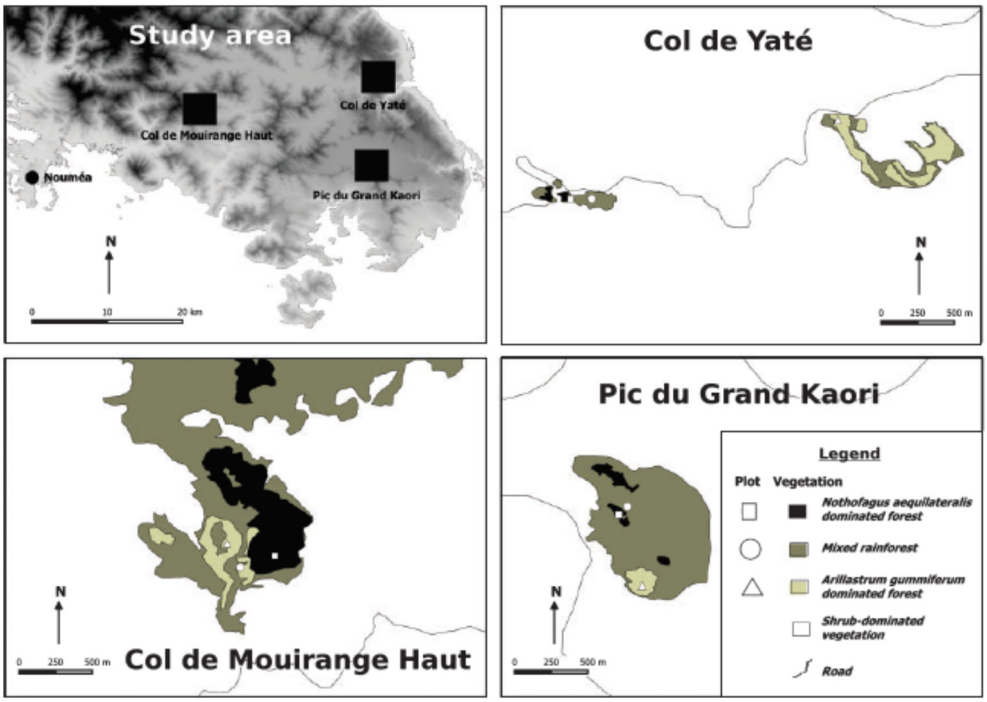

Fig. 2. Locations of the study sites and plots. The vegetation mapping is based on images interpretation. The grey background on the study area map represents the digital elevation model.

The location of each plot was chosen to be representative of the forest type in the site, without replication due to the limited extent of the forest patches.

These study sites were extensively described by Read *et al.* (2000) and the main characteristics of the sites and plots are summarised in Table 1. The Col de Mouirange Haut site was located on a south-west-facing slope, with the plot of *Arillastrum* forest located on the slope and crest of a hill. Selective logging occurred ~1900 in this area and there were a few very large old cut stumps on the plot. At the Col de Yaté site, the plot of *Arillastrum* forest was located on a south-facing slope surrounded by *maquis*, ~2 km east of the *Nothofagus* and mixed rainforest plots studied by Read *et al.* (2000). There was no evidence of human disturbance in this stand. At Pic du Grand Kaori, the plot of *Arillastrum* rainforest was situated at the base of a west-facing slope in the southern part of the forest at the edge with *maquis*. Despite the presence of an old logging track near the *Arillastrum* plot, no evidence of human activity was found within the stand.

Data collection

In each 0.25-ha plot in *Arillastrum* stands, all trees with a diameter at breast height (i.e. at 1.3 m, DBH) of ≥10 cm were inventoried, identified, tagged and their DBH measured. Smaller plants (DBH < 10 cm) were inventoried in subplots following Read *et al.* (2000). Thus, in 16 subplots of 10 m × 4 m (≈25% of the total plot area), the DBH of all woody plants ≥1.30 m high (i.e. saplings) was measured and *Arillastrum* trees were identified (Fig. S1, available as Supplementary material to this paper). All seedlings 0.03–1.29 m high were counted in a 2 m × 4 m subpart of the 16 subplots (≈5% of the total plot area) and *Arillastrum* seedlings were recorded (Fig. S1). The location of the 16 subplots was randomly chosen and was adjusted during field work so as to avoid overlap. Additionally, in each plot, 20 trees were randomly selected, consistent with the protocol applied by Read *et al.* (2000). The closest trees in the uppermost canopy were identified (*Arillastrum* or non-*Arillastrum*), allowing estimation of the proportion of *Arillastrum* foliage in the upper canopy.

Field work in *Arillastrum* forests occurred between April and October 2015. Most species were identified in the field, but in cases where identity was in doubt, samples were collected and identified by comparison with the collection of voucher specimens in IRD herbarium of Nouméa (NOU). Plant names follow FLORICAL nomenclature (Morat *et al.* 2012). Field work and sampling in *Nothofagus* forests and mixed rainforests were conducted by J. Read between 2008 and 2011 (resurveys of the plots reported in Read *et al.* 2000; and Read and Jaffré 2013). Table S1 (available as Supplementary material to this paper) summarises the parameters and sampling designs for the three different types of rainforest.

Data analysis

The dominance of *Arillastrum* and *Nothofagus* was evaluated using the relative density of canopy-level trees defined as the ratio

Table 1. Summary of study-sites characteristics

Site	Plot size (ha)	GPS coordinates	Altitude (m asl)	Upper-canopy dominance	Upper canopy (%)	Number of stems dominance (≥20 cm DBH)		Basal area ($m^2 ha^{-1}$)	Basal-area dominance	
						N. aequilateralis (%)	*A. gummiferum* (%)		*N. aequilateralis* (%)	*A. gummiferum* (%)
Col de Mouirange Haut										
Nothofagus forest	0.5	22.203142°S, 166.671611°E	295	*N. aequilateralis*	70	34.52	16.07	54.66	17.24	17.7
Arillastrum forest	0.25	22.201243°S, 166.669732°E	300	*A. gummiferum*	80	0	45.88	73.33	0	60.04
Mixed rainforest	0.5	22.20305°S, 166.670683°E	275	Mixed	0	1.24	28.57	64.26	0.8	27.3
Col de Yaté										
Nothofagus forest	0.1	22.16865°S, 166.893833°E	340	*N. aequilateralis*	95	82.93	0	51.03	50.84	0
Arillastrum forest	0.25	22.163369°S, 166.91132°E	270	*A. gummiferum*	75	0	38.2	52.66	0	49.22
Mixed rainforest	0.25	22.168428°S, 166.894858°E	350	Mixed with *N. balansae*	20	0	1.8	71.69	0	0.1
Pic du Grand Kaori										
Nothofagus forest	0.5	22.280278°S, 166.894658°E	260	*N. aequilateralis*	80	54.41	0	43.09	43.86	0
Arillastrum forest	0.25	22.285214°S, 166.896284°E	270	*A. gummiferum*	50	0	36.36	56.32	0	42.2
Mixed rainforest	0.5	22.279847°S, 166.895406°E	270	Mixed	0	0	0	54.47	0	0

between the number of stems of a given species and the total number of stems. A species is considered monodominant when this ratio is ≥0.5 (Connell and Lowman 1989). We also computed relative basal area to express dominance based on biomass, as suggested by Connell and Lowman (1989). Population dynamics were interpreted from the shape of histograms of DBH.

To assess whether monodominant forests were less diverse than were mixed-canopy rainforests, diversity analyses (Shannon diversity index and equitability) were performed. Only trees with ≥20-cm DBH were included to have comparable data (i.e. 100% inventory on the plot with DBH measurement and botanical identification; Table S1) between the nine plots in the three sites. To compare species richness among plots with different sample areas, we compiled rarefaction curves using the iNEXT R package (Chao *et al.* 2014; Hsieh *et al.* 2016), so as to standardise species richness by the sample size.

Non-metric multidimensional scaling (NMDS) was used to summarise variation in floristic composition among sites into two main axes, following computation of a Bray–Curtis dissimilarity matrix. To make comparable dissimilarities computed from plots with different sizes, a resampling procedure was applied. For each plot, we first estimated the mean number of stems ≥20 cm in DBH in 0.1 ha. We then used this mean value to build a randomly chosen 0.1-ha plot within a plot. This procedure was repeated 100 times per plot. The 0.1-ha random samples were then aggregated per plot to produce a resampled set of data for each plot. The relative proportions of basal area for each species were calculated for each plot. NMDS was then computed on this matrix. The ENVFIT function of vegan package for R (Oksanen *et al.* 2016) with 999 permutations was computed to assess the contribution of species to the NMDS. We used a permutational multivariate analysis of variance (PERMANOVA) using distance Bray–Curtis matrices to test the hypothesis that species composition differed among the three forest types. To explore floristic similarities among the different types of rainforest we also compiled Venn diagrams using the VennDiagram package for R (Chen 2016). To take into account the difference of field sampling effort for trees with a DBH of ≥20 cm and trees with a DBH of <20 cm and ≥10 cm, data were analysed separately. All statistical analyses were performed using the R 3.2.2. environment for statistical computing (R Core Team 2014).

Results

Structural characteristics

In all monodominant forest sites, the upper-canopy dominance of *Arillastrum* or *Nothofagus* was above 50%, but the upper-canopy dominance of *Arillastrum* was lower (50–80%) than was the dominance of *Nothofagus* (70–95%; Table 1). In terms of stem density (Fig. 3), the dominance of *Arillastrum* was never above 50%, in contrast to *Nothofagus* (Table 1). Monodominance of *Arillastrum* was more pronounced in terms of basal area, accounting for 42–60% of the total basal area, than was the 17–51% of the total basal area contributed by *Nothofagus* (Table 1, Fig. 4).

The DBH size structures differed strongly between *Arillastrum* and *Nothofagus* (Figs 3, 4). DBH distributions of *Arillastrum* were more plurimodal than those of *Nothofagus*. In addition, higher DBH values were recorded for *Arillastrum* than for *Nothofagus* at the three sites. At Col de Mouirange Haut site, one specimen of *Arillastrum* reached 146 cm, whereas the highest DBH recorded for *Nothofagus* was 54 cm at the same site.

No *Arillastrum* seedlings and only one sapling were observed in the three studied *Arillastrum* forests (Table 2). In contrast, in *Nothofagus* forests, the seedlings of the dominant species accounted for more than 50% of the total number of seedlings (Table 2). In addition, the total numbers of seedlings in *Arillastrum* and mixed forests were one-third of those in *Nothofagus* forests (Table 2).

Floristic diversity and composition

Observed species richness was higher in *Nothofagus* forests (72 species) than in *Arillastrum* forests (39 species). *Arillastrum* forests and *Nothofagus* forests shared 23 species (Fig. 5*a*). *Nothofagus* forests shared 35 species with mixed rainforests, whereas *Arillastrum* forests shared only 17 species with the latter. In contrast, for trees with 10 cm ≤ DBH < 20 cm, among the 157 species identified in the three sites, highest species richness and specificity were found in *Arillastrum* forests (Fig. 5*b*).

When comparing expected species richness for trees with DBH of ≥20 cm in both *Arillastrum* forests (20 species per plot on average) and *Nothofagus* forests (22 species per plot on average), we found lower values than the species richness in mixed rainforests (34 species per plot on average; Table 3). Tree species richness in *Arillastrum* forests was different from that in *Nothofagus* forests and mixed rainforests, except at Pic du Grand Kaori (Fig. 6). However, the influence of the forest type remained unclear. For trees with 10 cm ≤ DBH < 20 cm, the observed species richness in *Arillastrum* forests (39 species) was higher than that in the two other types of rainforests (Table 3). In contrast, *Nothofagus* forests showed a much lower equitability than did *Arillastrum* and mixed rainforests (Table 3).

The NMDS (Fig. 7*a*) and the associated PERMANOVA (Table 4) suggested that the floristic composition and abundance differed among the three forest types. However, these differences were due to the two dominant species (Table 5). Indeed, when NMDS was computed without *Nothofagus* and *Arillastrum*, no significant differences in floristic composition among the three forest types were found (Fig. 7*b*). Instead, the site explained 38% (P-value = 0.009) of the dissimilarity in floristic composition, using basal area (Table 4).

Discussion

Monodominance, structure and floristic diversity

Both *Arillastrum* and *Nothofagus* were monodominant in the canopy layer, but the structure of their monodominance was very different. The monodominance of *Nothofagus* was characterised by a high number of stems in the lower DBH classes (>30 cm), whereas for *Arillastrum*, it was characterised by fewer but larger stems, resulting in a higher dominance in terms of basal area. Despite these differences, the general structural parameters (e.g. basal area and stem density) of the monodominant forests did not differ from those of mixed forests on ultramafic substrates in New Caledonia (Ibanez *et al.* 2014). For instance, the basal area of *Arillastrum* forests ranged from 52.7 to 73.3 $m^2 ha^{-1}$ in our study, which was comparable to values recorded in the 20 × 20 m plots

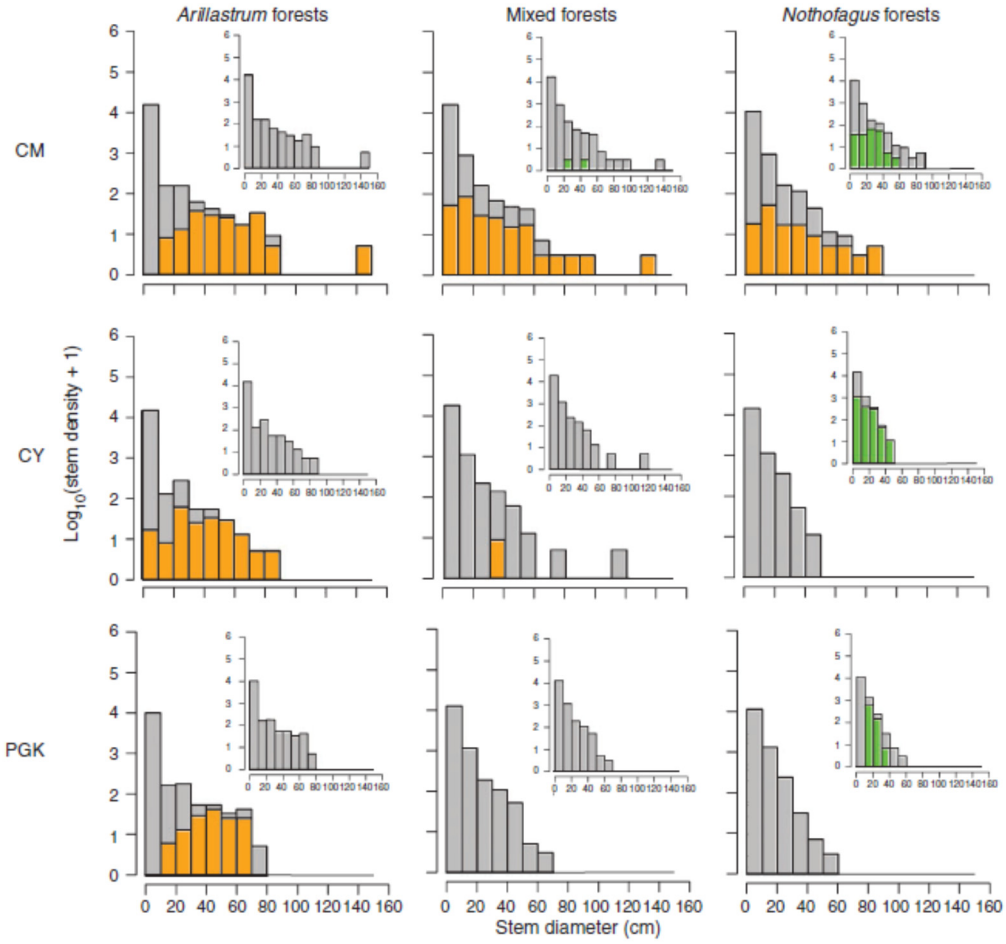

Fig. 3. Stem density with respect to diameter-size classes. Forest types are represented vertically and study sites horizontally. For each plot, large histograms focus on *Arillastrum gummiferum*, whereas small histograms focus on *Nothofagus aequilateralis*. Grey, orange and green represent the total population of *A. gummiferum* and *N. aequilateralis*, respectively. Only plants ≥1.3 m high are included. CM, Col de Mouirange Haut; CY, Col de Yaté; PGK, Pic du Grand Kaori.

of the New Caledonian Plant Inventory and Permanent Plot Network, i.e. $60.5 \pm 19.75\,m^2\,ha^{-1}$ (Ibanez *et al.* 2014).

Species richness and diversities in *Nothofagus* and *Arillastrum* forests were not lower than those observed in mixed rainforest. When removing *Nothofagus* and *Arillastrum* from the inventories, the floristic compositions between the three forest types did not differ significantly. Our results support previous studies that suggested that species richness, species diversity and floristic composition are not so different in monodominant forests and adjacent mixed forests (Beard 1946; Hart 1990; Read *et al.* 2000). Thus, monodominance does not necessarily limit diversity.

Transient monodominance of Nothofagus *and* Arillastrum

Nothofagus is an irregular-flowering and mass-fruiting species (Read and Hope 1996). The ability of its seedlings to establish under its own cover suggests that monodominance can persist over several generations. Yet, seedlings of *Nothofagus* require canopy openings to become saplings (Read *et al.* 2015), and population-size structures generally show evidence of episodic regeneration, suggesting that disturbance is necessary to explain their establishment and persistence (Read and Jaffré 2013). We suggest that the occurrence of seedlings in a shaded understorey could be explained by the ectomycorrhizal status of *Nothofagus*. Indeed, a survivorship advantage might be provided to the seedlings of *Nothofagus* through transfer of carbon, nitrogen and phosphorus from adults through interconnecting mycelia (Simard and Durall 2004; McGuire 2007). The poor dispersal of seeds (Read and Hope 1996), the relative shade intolerance of seedlings, the long lifespan (>100 years) of the species and the disturbance hypothesis through large cyclones (Read and Jaffré 2013) match with the transient dominance proposed by Newbery

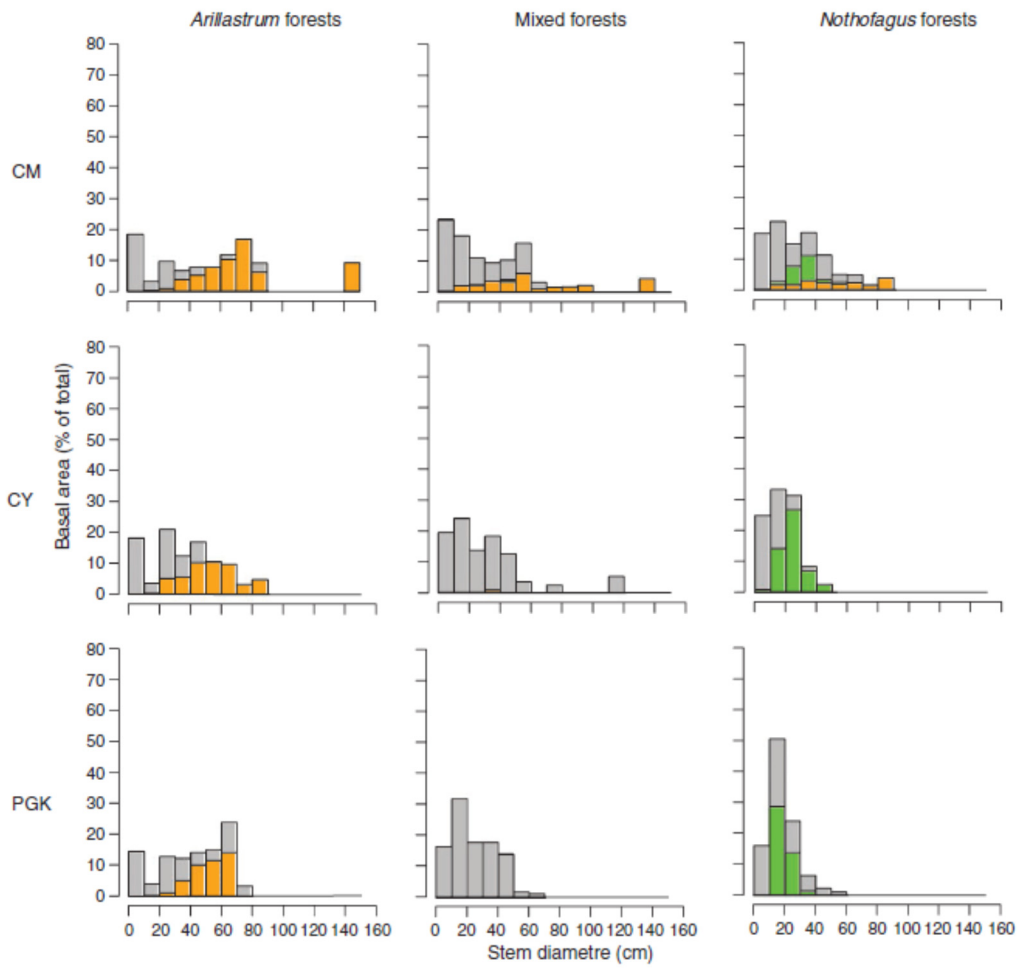

Fig. 4. Basal area with respect to diameter size classes. Forest types are represented vertically and study sites horizontally. Grey refers to the total population, orange to *Arillastrum gummiferum* and green to *Nothofagus aequilateralis*. Only plants ≥1.3 m high are included. CM, Col de Mouirange Haut; CY, Col de Yaté; PGK, Pic du Grand Kaori.

Table 2. Seedlings and proportions of *Arillastrum gummiferum* and *Nothofagus aequilateralis* at the different sites
n.a., not available

Site	Number of plots	Mean number of seedlings per plot	% of *N. aequilateralis* seedlings	% of *A. gummiferum* seedlings
Col de Mouirange Haut				
Nothofagus forest	15	44±27	58	0
Arillastrum forest	16	28±20	n.a.	0
Mixed rainforest	15	17±8	0	0
Col de Yaté				
Nothofagus forest	10	194±136	84	0
Arillastrum forest	15	57±30	n.a.	0
Mixed rainforest	15	60±41	9	0
Pic du Grand Kaori				
Nothofagus forest	12	188±153	55	0
Arillastrum forest	16	51±26	n.a.	0
Mixed rainforest	12	81±22	0	0

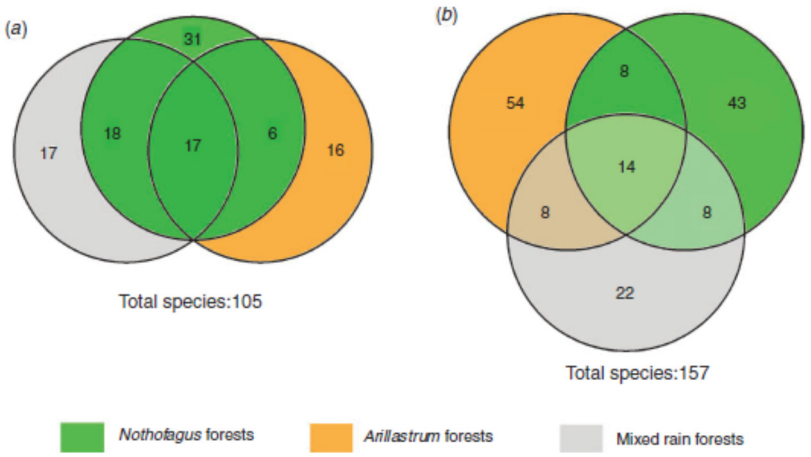

Fig. 5. Venn diagrams for all sites for the three types of forests. (*a*) DBH ≥20 cm; (*b*) 10 cm ≤ DBH < 20 cm.

Table 3. Species richness and diversity at the different sites

Species richness was calculated with iNEXT for 40 and 200 individuals. Values in brackets are for lower and upper limits of the interval of confidence at 95%

Site	Species richness (<20-cm DBH)	Species richness (≥20-cm DBH)	Diversity (H) (≥20-cm DBH)	Equitability (E) (≥20-cm DBH)	Species richness (≥20-cm DBH) (*n* = 40)	Species richness (≥20-cm DBH) (*n* = 200)
Col de Mouirange Haut						
Nothofagus forest	35	41	2.62	0.71	16.3 [14.2; 18.3]	45.3 [37.2; 53.5]
Arillastrum forest	36	16	2.05	0.74	12.5 [10.9; 14.1]	17.1 [11.5; 22.6]
Mixed rainforest	34	44	2.87	0.76	18.5 [16.1; 20.9]	49.7 [41.4; 58]
Col de Yaté						
Nothofagus forest	11	5	0.65	0.41	4.9 [3.1; 6.8]	7.9 [4.6; 11.2]
Arillastrum forest	32	18	2.23	0.77	12.8 [11.1; 14.4]	21.9 [15.7; 28.2]
Mixed rainforest	39	29	2.86	0.85	17.4 [15.1; 19.7]	37.2 [28.7; 45.7]
Pic du Grand Kaori						
Nothofagus forest	18	20	1.86	0.62	11.4 [9.7; 13.1]	24 [16; 32.1]
Arillastrum forest	50	25	2.45	0.76	15.7 [12.7; 18.6]	39.9 [25.4; 54.4]
Mixed rainforest	18	29	2.5	0.74	14.3 [11.9; 16.7]	30.6 [24.5; 36.7]

et al. (2013; i.e. monodominance of poorly dispersed species needs disturbances).

Arillastrum would be another case of transient dominant species that needs disturbances to persist. The monodominance of *Arillastrum* was characterised by the absence of seedlings of this species. This, together with the absence of reverse-J population-size structures that typify the non-continuously regenerating populations (Zedler and Goff 1973), suggest that its dominance could not persists beyond one generation (Type II, according to Connell and Lowman 1989). However, the DBH distribution of *Arillastrum* at the three sites was plurimodal and suggests the subsequent establishment of different cohorts. For instance, at Col de Mouirange Haut, the DBH class 70–80 cm is likely to correspond to one cohort and the DBH classes 30–50 cm to another cohort. On the basis of growth-rate estimations from Papineau (1989), we can estimate that these two cohorts would have established ~250 and 60 years ago respectively, with the largest *Arillastrum* measured (146-cm DBH) being ~400 years old. This suggests that almost 200 years were necessary to meet the conditions required for the establishment of a new *Arillastrum*

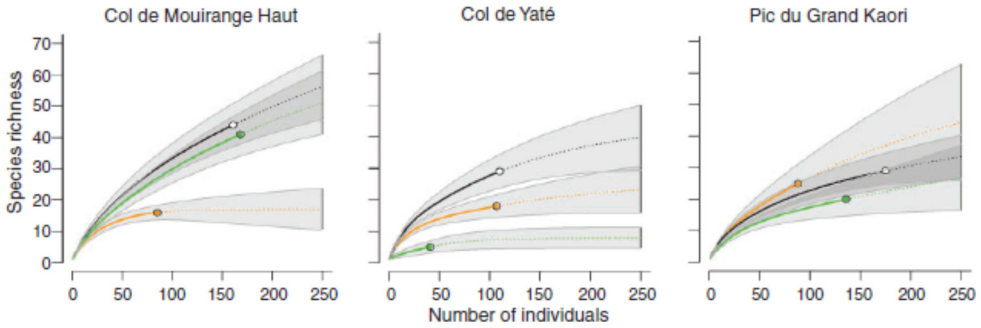

Fig. 6. Rarefaction curves for the three types of forests in the three study sites for DBH ≥20 cm. Black for mixed rainforests, orange for *Arillastrum* forests and green for *Nothofagus* forests. Plain lines indicate interpolation, dashed lines indicate extrapolation and circles represent the observed species richness.

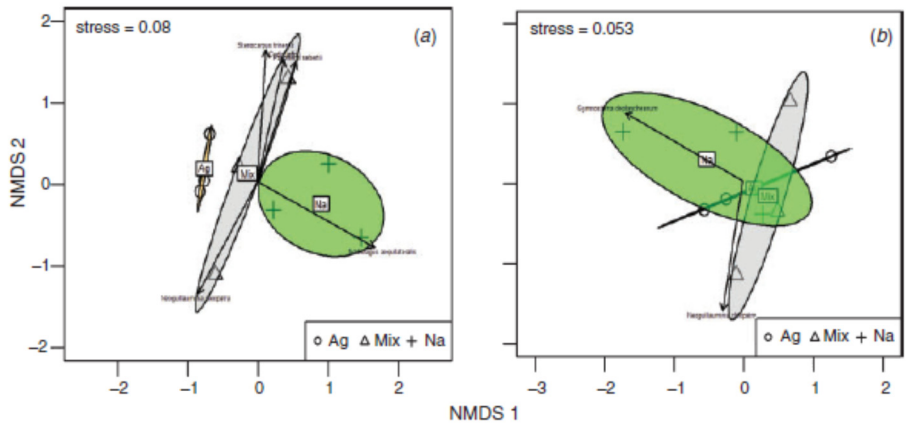

Fig. 7. Non-metric multidimensional scaling configuration plots using resampled dataset for DBH ≥20 cm, (*a*) with *Arillastrum gummiferum* and *Nothofagus aequilateralis*; (*b*) without *A. gummiferum* and *N. aequilateralis*. Grey for mixed rainforests (Mix), orange for *Arillastrum* forests (Ag) and green for *Nothofagus* forests (Na). Only species with *P*-value of <0.05 are indicated with arrows.

Table 4. Results of permutational multivariate analysis of variance (PERMANOVA) on dissimilarity in floristic composition, with or without *Arillastrum gummiferum* and *Nothofagus aequilateralis* included in the resampled dataset for DBH ≥20 cm
Significant *P*-values are shown in bold

Parameter	d.f.	Sums of squares	Mean squares	*F*.model	R^2	*P*-value (>*F*)
PERMANOVA with *A. gummiferum* and *N. aequilateralis*						
Site	2	0.70	0.35	2.37	0.27	**0.030**
Forest formation	2	1.28	0.64	4.29	0.50	**0.001**
Residuals	4	0.59	0.15	0.23		
Total	8	2.57	1.00			
PERMANOVA without *A. gummiferum* and *N. aequilateralis*						
Site	2	1.04	0.52	1.90	0.38	**0.009**
Forest formation	2	0.63	0.31	1.15	0.23	0.280
Residuals	4	1.09	0.27	0.40		
Total	8	2.75	1.00			

Table 5. Major species contributing to dissimilarity among rainforest types derived by non-metric multidimensional scaling (NMDS), with *Arillastrum gummiferum* and *Nothofagus aequilateralis*
Resampled dataset for DBH of ≥20 cm was used

Species	r^2	*P*-value (>*r*)
Nothofagus aequilateralis	0.90	0.001
Stenocarpus trinervis	0.70	0.023
Pancheria sebertii	0.65	0.034
Codia jaffrei	0.61	0.036
Neoguillauminia cleopatra	0.62	0.037
Flindersia fournieri	0.60	0.071
Montrouziera gabriellae	0.57	0.075
Arillastrum gummiferum	0.56	0.077
Sparattosyce dioica	0.58	0.082
Archidendropsis granulosa	0.58	0.083

cohort under the former cohort. Additionally, *Arillastrum* shares ecological traits with *Nothofagus*; the species is also poorly dispersed (Papineau 1989), ectomycorrhizal and its seedlings are considered shade-intolerant (Read *et al.* 2015).

Ecological strategies of Nothofagus *and* Arillastrum *to maintain their monodominance*

In New Caledonia, cyclones and wildfires are likely to be the main disturbances that open the canopy and favour the regeneration of shade-intolerant species (Read and Jaffré 2013). Considering the lifespan of *Nothofagus* (>100 years; Read and Jaffré 2013) and the regional cyclone regime (one tropical depression or cyclone per year on average), it is very likely that populations would experience large-scale disturbances within their lifetime (Read and Jaffré 2013). The stock and proportion of *Nothofagus* seedlings observed in the understorey of *Nothofagus* forests could be a way to mitigate the irregular flowering and fruiting of the species. Cyclones open the canopy by leaf, branch and tree falls. This constitutes a great opportunity for light-demanding species when their seedlings are already established in the understorey. Therefore, we suggest that the investment of *Nothofagus* in the maintenance of an abundant bed of seedlings would be a strategy to rapidly colonise gaps created by cyclones. The putative facilitation processes between adults and seedlings *of Nothofagus* through mycorrhizal networks, in association with disturbance, might provide a competitive advantage that promotes persistence of monodominance (Peh *et al.* 2011).

We propose a different ecological strategy for the persistence of *Arillastrum* monodominance based on wildfire disturbance. Monodominance could be promoted by a competitive advantage such as adaptation to the frequency of wildfires. For instance, Ibanez and Birnbaum (2014) described the case of monodominant *Codia* species at the edge of rainforest in fire-prone landscape of New Caledonia. *Arillastrum* has a combination of traits that could allow the species to survive some wildfire regimes. On the basis of data from Papineau (1989), we established the allometry between bark thickness (BT) and DBH of *Arillastrum* (BT (in cm) = 0.23345 DBH (in cm)$^{0.4229}$ with $r^2 = 0.8561$). The allometric coefficient can be interpreted as an allocation coefficient (Jackson *et al.* 1999). With an allometric coefficient of 0.42, *Arillastrum* has a thick bark, and its investment in BT is disproportionally higher when the trees are small, which is a strategy reported to protect against fire (Ibanez *et al.* 2013; Jackson *et al.* 1999). In addition, *Arillastrum* is known to resprout after fires in natural forest stands (Papineau 1989), which is a common trait of pyrophyte species (Higgins *et al.* 2000; Bell 2001; Vesk 2006), but uncommon for mid- or late successional trees (McCoy *et al.* 1999). Thus, *Arillastrum* has the ability to survive some wildfire regimes, which is consistent with the frequent presence of charcoal in the soil of *Arillastrum* as well as callus on their trunks (J. Demenois pers. obs.). In New Caledonia, fires mainly occur between August and November and the flowering and fruiting of *Arillastrum* occur between October and February, and April and August, respectively (Bailly *et al.* 1986). The viability of the seeds is limited to 6–9 months (Bailly *et al.* 1986). Hence, *Arillastrum* does not invest in a soil seed bank, but rather relies on the probability that the surviving trees seed after a wildfire. Curt *et al.* (2015) estimated that, in New Caledonia, *maquis* and forest on ultramafic substrates are burnt at least every 35 and 480 years respectively. In addition, Perry and Enright (2002) assessed that more than 400 years without fire are necessary for the establishment of forest on a burnt area; *Arillastrum* has the ability to grow in rainforest but also in *maquis* (Jaffré 1980). Because of its long lifespan, it is likely that *Arillastrum* populations would experience wildfire disturbances within their lifetime, allowing regeneration and maintenance of dominance if the wildfire regime is compatible with the fire resistance of the species.(Curt *et al.* 2015)

Finally, we suggest that the presence of *Arillastrum* is an indicator of the past and current location of edges between *maquis* and forests. Its ability to resist some wildfire regimes is likely to give it a competitive advantage to slowly colonise *maquis* from the edge of *Arillastrum* forest. In terms of succession, *Arillastrum* forests would be a step between ligno-herbaceous *maquis* and mixed rainforest.

Conclusions

Our results support the hypothesis that monodominance of *Arillastrum* and *Nothofagus* are both examples of transient dominance; yet, additional plots and long-term surveys would be needed to confirm our findings. Disturbances are necessary to allow these poorly dispersed species to regenerate under their own shade and for their dominance to persist. The persistence of *Arillastrum* is likely to rely on disturbance by fires, whereas the persistence of *Nothofagus* would rely on disturbance by cyclones. *Nothofagus* forests are secondary forests successional to mixed rainforests (Read and Jaffré 2013), whereas *Arillastrum* forests would colonise and succeed ligno-herbaceous *maquis* and precede the establishment of mixed rainforests.

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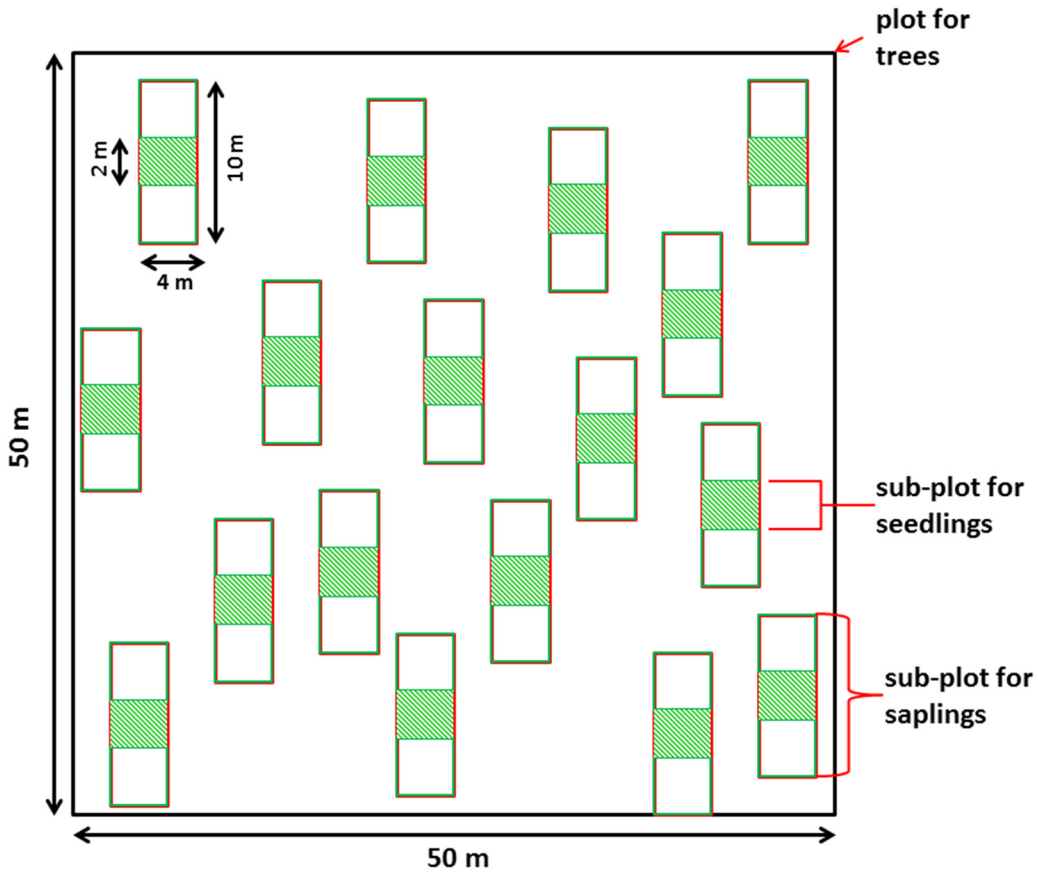
Supplementary materials

Supplementary Fig.1. Sampling design in each 50 m x 50 m plot



Supplementary Table 1. Sampling design and data collected in each sites

	Seedlings	Saplings [0-10 cm[DBH	Small trees [10-20 cm[DBH	Trees ≥ 20 cm DBH
Arillastrum forest				
Plot area (m^2)	8	40	2 500	2 500
Number of plots	48	48	3	3
Diameter at breast height	X	√	√	√
Botanical identification	X *Arillastrum gummiferum* vs other species	X *Arillastrum gummiferum* vs other species	√	√
Nothofagus forest				
Plot area (m^2)	8	40	40	Between 1 000 and 5 000
Number of plots	37	37	37	3
Diameter at breast height	X	√	√	√
Botanical identification	√	√	√	√
Mixed rain forest				
Plot area (m^2)	8	40	40	Between 1 000 and 5 000
Number of plots	42	42	42	3
Diameter at breast height	X	√	√	√
Botanical identification	√	√	√	√
X : not measured or collected				
√ : measured or collected				

Chapitre 3 – Quelle influence des traits racinaires des communautés végétales et des symbioses mycorhiziennes sur la stabilité des agrégats des Ferralsols sur substrats ultramafiques ?

Ce chapitre a donné lieu à la soumission de deux articles, respectivement dans les revues *Ecological Engineering* et *Plant and Soil* :

- Demenois J., Carriconde F., Rey F., Stokes A., *Tropical plant communities modify soil aggregate stability along a successional vegetation gradient on a Ferralsol,* accepté dans Ecological Engineering ;
- Demenois J., Rey F., Stokes A., Carriconde F., *Linkages between root traits, soil fungi and aggregate stability in tropical plant communities along a successional vegetation gradient,* soumis à Plant and Soil.

La finalité de ce travail était d'étudier l'influence des traits racinaires des communautés végétales et des symbioses mycorhiziennes sur la stabilité des agrégats. Pour ce faire, nous nous sommes intéressés à des formations végétales largement répandues dans les paysages de l'archipel et constituant une succession végétale potentielle caractéristique des Ferralsols sur substrats ultramafiques : maquis ligno-herbacé dégradé par les feux à répétition > maquis ligno-herbacé à *Tristaniopsis glauca* > forêt monodominante à *Arillastrum gummiferum* > forêt monodominante à *Nothofagus aequilateralis* > forêt mixte. Dans les milieux érodés, les changements de composition floristique des communautés végétales seraient un facteur-clé de leur restauration (Walker and del Moral 2009) d'où la pertinence de se placer le long d'un gradient de succession végétale. De plus, plusieurs études récentes menées sous différents climats (semi-aride, méditerranéen ou continental) ont mis en évidence une augmentation de la stabilité des agrégats au fur et à mesure des successions végétales (Cheng *et al.* 2015; Erktan *et al.* 2016; Lin *et al.* 2014; Qiu *et al.* 2015). Pour autant, les influences des traits racinaires et des champignons demeurent complexes et finalement largement méconnues. Dans nos conditions en milieu naturel, la stabilité des agrégats n'ayant jamais été évaluée, le travail a tout d'abord consisté à caractériser celle-ci pour chaque formation végétale. Une fois cette caractérisation réalisée, nous avons procédé à l'exploration de l'influence des traits racinaires et des symbioses mycorhiziennes sur la stabilité des agrégats.

Ainsi, les objectifs scientifiques de ce travail étaient doubles :

- étudier l'influence des communautés végétales sur la stabilité des agrégats des Ferralsols sur substrats ultramafiques dans un premier temps ;

- puis identifier les facteurs abiotiques et biotiques influençant la stabilité des agrégats.

Les principaux résultats de ce travail sont les suivants :

- la stabilité des agrégats des Ferralsols sur substrats ultramafiques est élevée (> 2 mm), y compris dans les maquis ligno-herbacés dégradés par les feux à répétition, probablement du fait des fortes teneurs en sesquioxydes de fer et d'aluminium (> 35 %) dont la formation est accentuée par les feux ;
- la stabilité des agrégats est influencée par la couverture végétale et la composition floristique. Elle augmente depuis les maquis ligno-herbacés dégradés jusqu'aux forêts ;
- les racines fines et la longueur de racine par unité de volume (Root Length Density) ont un impact direct et positif sur la stabilité des macro-agrégats tandis que le carbone organique du sol l'influence indirectement. *A contrario*, la longueur de racine par masse de racine (Specific Root Length) est corrélée négativement avec la stabilité des agrégats ;
- la biomasse fongique, et donc les symbioses mycorhiziennes, ont un impact direct et positif sur la stabilité des macro-agrégats ;
- trois espèces végétales sont suspectées d'avoir potentiellement un impact positif sur la stabilité des agrégats : *Costularia arundinacea*, *Garcinia amplexicaulis* et *Myodocarpus fraxinifolius*. Néanmoins, les contributions des espèces dominantes et ectomycorhizées que sont *Tristaniopsis glauca*, *Arillastrum gummiferum* et *Nothofagus aequilateralis* ne peuvent être exclues.

Ce travail a ainsi permis de suggérer l'existence d'un seuil biotique (Hobbs and Harris 2001) entre les maquis ligno-herbacés dégradés et les maquis ligno-herbacés. Les feux répétés seraient la cause principale de cette dégradation (Curt *et al.* 2015) et du franchissement de ce seuil qui *in fine* limite le développement de la végétation. L'augmentation de la biomasse végétale constitue en effet le facteur-clé contribuant à accroître la stabilité des agrégats entre ces deux stades. Ainsi, la protection contre les feux, associée à la promotion des successions végétales à travers l'utilisation d'espèces potentiellement facilitatrices comme *C. arundinacea*, pourrait constituer une stratégie efficiente pour limiter l'érosion des Ferralsols et améliorer leur fonctionnalité. De plus, l'influence des communautés végétales et fongiques sur la stabilité des agrégats des Ferralsols sur substrats ultramafiques a été clairement mise en exergue, sans toutefois que l'on puisse distinguer l'influence des symbioses mycorhiziennes de celle des autres champignons.

Ainsi, dans le chapitre suivant nous nous intéressons à l'effet de l'inoculation contrôlée avec des champignons mycorhiziens (AMF et ECM) sur la stabilité des agrégats. De plus, dans l'optique d'identifier de potentielles espèces-outils pour accroître la stabilité des agrégats des Ferralsols sur substrats ultramafiques *via* des actions de restauration écologique, un focus sur l'influence des traits racinaires et des communautés fongiques associées est fait sur *C. arundinacea*, *T. glauca* et *A. gummiferum* en conditions *in situ*.

Tropical plant communities modify soil aggregate stability along a successional vegetation gradient on a Ferralsol

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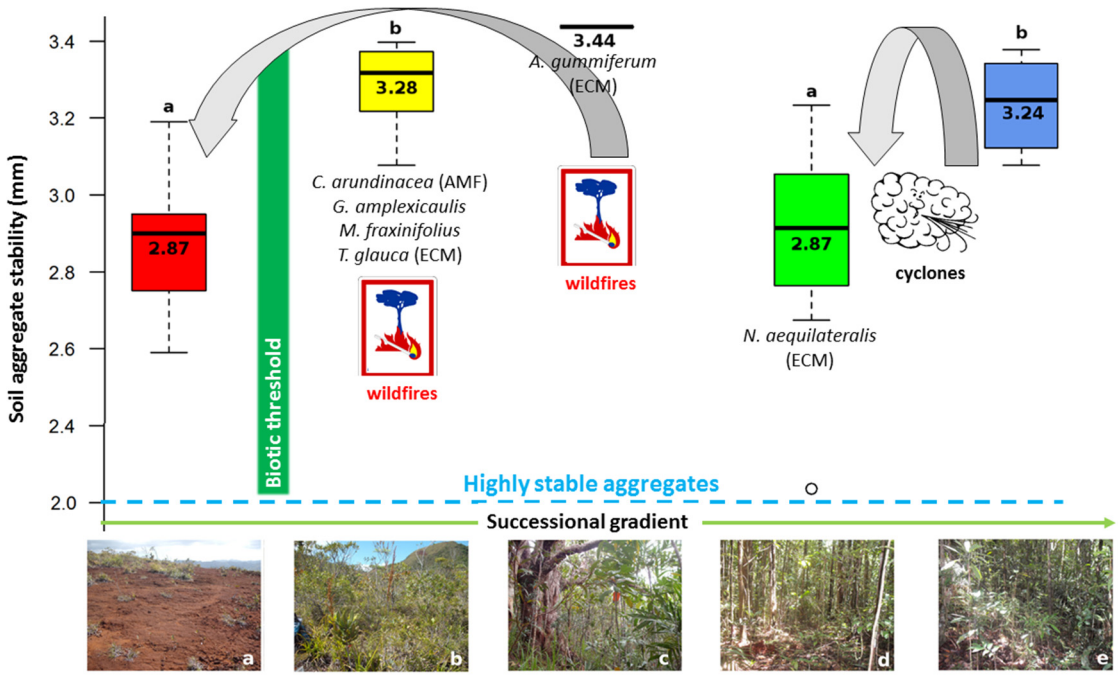
Abstract

Soil aggregate stability is viewed as a promising indicator of the restoration status in eroded ecosystems, where the change in plant community composition through successional dynamics is a key driver of ecosystem restoration. In many tropical regions, ecological restoration is an important issue, but the relationship between different types of plant communities and soil aggregate stability is poorly understood. We examined how tropical plant communities modified soil aggregate stability along a successional vegetation gradient on a Ferralsol in New Caledonia. We identified five plant communities, ranging from an early (sedge dominated ecosystems) to a late successional stage (well-established, dense, mixed rainforest). Aggregate stability, total soil organic carbon (SOC) and iron and aluminium sesquioxides were measured in soil originating from each community. Results showed that aggregate stability of the Ferralsol was very high, even on eroded sites, likely due to the high levels of iron and aluminium sesquioxides also found. The levels of iron sesquioxides were particularly high (>10%), due partly to the frequency of wildfires in the region. Total SOC increased from sedge-dominated communities (<1%) to mixed rainforest (>3.5%). Aggregate stability was modified by plant cover and community composition and increased from sparse, early successional vegetation to late successional dense, mixed rainforest. Our study showed that certain plant species have a positive impact on soil aggregate stability and should be considered for ecological restoration on Ferralsols. e.g., *Costularia arundinacea*, *Garcinia amplexicaulis* and *Myodocarpus fraxinifolius*. In conclusion, we suggest that vegetation dynamics should be taken into account when investigating changes in aggregate stability in a context of ecosystem restoration.

Graphical abstract



Highlights

- Soil aggregate stability of tropical Ferralsols in New Caledonia was very high in the five plant communities studied, probably due to the high content of iron sesquioxides often formed in soil after wildfires.
- Along the successional gradient of vegetation, aggregate stability was modified by plant cover and community composition and increased from sparse vegetation to rainforest.
- *Costularia arundinacea*, *Garcinia amplexicaulis* and *Myodocarpus fraxinifolius* have a positive impact on soil aggregate stability and should be considered for ecological restoration on Ferralsols.

- Vegetation dynamics should be taken into account when investigating changes in aggregate stability.

Keywords

Aggregate stability, plant community composition, vegetation dynamics, ecological restoration, ultramafic substrates, New Caledonia.

1. Introduction

Soil aggregates are naturally occurring clusters or group of soil particles in which the forces holding the particles together are much stronger than the forces between the adjacent aggregates (Martin *et al.* 1955). Clustering and stabilization of soil particles in aggregates are complex processes (Six *et al.* 2004), influenced by soil characteristics (e.g. abiotic and biotic factors), vegetation (e.g. plant cover, fine root density), land management and climate (Bronick and Lal 2005; Six *et al.* 2004). Aggregate stability is a measure of the erodibility of a soil and is defined as the extent to which soil aggregates resist falling apart when wetted by and hit by rain drops (Le Bissonnais 1996). Aggregate stability is seen as a key ecosystem process influencing carbon storage (Jastrow *et al.* 1998), nutrient availability (Wang *et al.* 2001) and resistance to erosion (Barthès and Roose 2002). Among the numerous biotic factors, plant fine root density and mycorrhizal activity play crucial roles in aggregate stability (Graf and Frei 2013; Leifheit *et al.* 2014b; Rillig and Mummey 2006; Tisdall and Oades 1982). Thus, aggregate stability is viewed as a promising indicator of the restoration status of the site in eroded ecosystems (Burri *et al.* 2009).

In eroded ecosystems, the change in plant community composition through successional dynamics is a key driver of their restoration (Walker and del Moral 2009). Several recent studies in sub-arid, Mediterranean or continental climates showed that aggregate stability increased along a successional gradient of vegetation (Cheng *et al.* 2015; Erktan *et al.* 2016; Lin *et al.* 2014; Qiu *et al.* 2015). In many tropical regions, such as New Caledonia, an archipelago in the south west Pacific ocean, ecological restoration is a major issue, especially on heavily eroded sites (Losfeld *et al.* 2015). Yet despite the increasing number of studies focusing on ecosystem restoration, soil aggregate stability remains a poorly understood

process, and it is not known how stability is modified by tropical plant community composition.

The New Caledonia archipelago is currently the fifth producer of nickel in the world (US Geological Survey 2016), and nickel mining is one of the main causes of soil erosion (Dugain 1953). Nickel mining will remain a major component of the island's economy in the coming decades, therefore programs aim at identifying suitable techniques for ecological restoration, as well as key indicators of success. Soils in the region are also prone to water erosion in areas denuded by deforestation and forest fires. Water erosion is the most significant cause of the degradation of lagoon ecosystems and fringing reefs, in particular during cyclonic floods (Dumas *et al.* 2010). A better quantification and mapping of potential erosion hotspots would improve management strategies, and soil aggregate stability could be used as an indicator of erodibility. However, to our knowledge, no studies exist providing evidence that aggregate stability could be used as a proxy for erodibility of tropical ultramafic soils such as those found in New Caledonia.

Apart from providing major nickel reserves, ultramafic substrates in New Caledonia also host a unique terrestrial biodiversity. A total of 1160 plant species, 95 % of which are endemic to New Caledonia, are strictly restricted to ultramafic areas (L'Huillier *et al.* 2010), highlighting the necessity to preserve and manage soils hosting this unique flora (Isnard *et al.* 2016).

Soils derived from ultramafic substrates in New Caledonia are found mainly in the south of the main island (Schmid 1982), where vegetation is represented by sclerophyllous shrubland formations (called maquis), and to a lesser extent by patches of rainforest (L'Huillier *et al.* 2010). The shrublands are floristically diverse and can be dominated by a single or several

104 species, e.g. *Tristaniopsis* spp. (L'Huillier *et al.* 2010). These communities represent mostly
105 secondary vegetation resulting from the degradation of the initial rainforests (Isnard *et al.*
106 2016). As successional phases progress, shrubland develops into rainforest, e.g. mixed
107 rainforests or ectomycorrhizal monodominant rainforests (i.e. a forest where ≥ 50% of the
108 canopy trees' cover, or basal area, or stems, or biomass, belongs to a single species (Connell
109 and Lowman 1989)). *Nothofagus aequilateralis* (Nothofagaceae) and *Arillastrum gummiferum*
110 (Myrtaceae), two endemic tree species, commonly form monodominant rainforests on this
111 part of the main island (Read and Jaffré 2013).

112 In this study, we examined how tropical plant communities modified soil aggregate stability
113 along a successional vegetation gradient on a Ferralsol in New Caledonia. We investigated
114 five plant communities, representing five phases of vegetation succession. Communities
115 ranged from sedge dominated ecosystems to well-established mixed rainforest. Results
116 allowed us to identify potentially suitable plant species for restoring eroded soils and to
117 determine if aggregate stability is a valid proxy for soil erodibility in New Caledonia.

118

119 ## *2.* Materials and methods

120 ### *2.1. Field sites*

121 Studies were performed on two field sites located in the Massif du Grand Sud in New
122 Caledonia (Fig. 1). The first site, called La Rivière Blanche (22°9'S-166°41'E), is part of the
123 Rivière Bleue Provincial Park. At the beginning of the 20th century, chromium mining and
124 forestry were the main economic activities in the area, but have since been stopped. The
125 second site, called Bois du Sud (22°10'S-166°46'E), is part of a botanical reserve created in

126 2009. From the 1940s until late 1980s, logging of *Arillastrum gummiferum* occurred in the
127 area. The two sites are only eight kilometres apart and are located at an altitude between 300
128 and 500 m. Mean annual precipitation is 3000 mm and the minimal and maximal mean annual
129 temperatures are 20.5 °C and 26.6 °C (Météo France 2016b). Both sites were selected
130 according to three main criteria: (i) ultramafic substrates characteristic of the Massif du Grand
131 Sud, (ii) sites comprised a Ferralsol with a slope <30° and (iii) plant communities were typical
132 of the ultramafic landscape and represented different successional vegetation stages.

133

134 *1.1. Successional stages of vegetation*

135 Five types of plant communities were examined:

136 (i) Sedge dominated communities with dominance of *Costularia nervosa* and *C.*
137 *arundinacea* (Cyperaceae). These communities arise largely as a result of
138 repeated shrubland fires. In these communities, sedges make up 15 % of
139 ground cover and are considered as an early successional stage (Fig. 2a).
140 (ii) *Tristaniopsis glauca* (Myrtaceae) (Fig. 2b) growing in open sclerophyllous
141 shrubland with a maximum height of less than 2 – 3 m (Jaffré 1970).
142 *Tristaniopsis glauca* is ubiquitous in shrublands of the Massif du Grand Sud and
143 is associated with ectomycorrhizal fungi (Amir and Ducousso 2010).
144 (iii) Monodominant *Arillastrum gummiferum* rainforest which succeeds the
145 sclerophyllous shrubland stage (Fig. 2c) (Demenois *et al.* (2017b). *Arillastrum*
146 *gummiferum* usually occurs in extensive, monodominant stands (Sebert 1874;
147 Virot 1956). The monodominance seems to persist because of frequent

148 disturbance by wildfires (Demenois *et al.* 2017b). *Arillastrum gummiferum* is
149 monotypic, endemic to New Caledonia and belongs to a sister lineage of the
150 Australian eucalypt group (Ladiges and Cantrill 2007). *A. gummiferum* grows
151 exclusively on ultramafic substrates and is associated with ectomycorrhizal
152 fungi (Papineau 1989).

153 (iv) Monodominant *Nothofagus aequilateralis* rainforest, which is an early
154 successional forest (Fig. 2d) (Read and Jaffré 2013), forming monodominant
155 stands (Read and Hope 1996). Cyclone disturbances may be involved in the
156 establishment and persistence of *Nothofagus* rainforests, at least at low or
157 mid-elevations (Read and Jaffré 2013). *Nothofagus aequilateralis* is endemic to
158 New Caledonia, occurs on ultramafic substrates and is associated with
159 ectomycorrhizal fungi (McCoy 1991).

160 (v) Mixed rainforest, which is defined as a forest that is not dominated at its
161 canopy by a single tree species (Fig. 2e). Nevertheless, plant species known to
162 typically form monodominant stands can also be present, but as isolated trees.

163

164 *1.2. Plant community composition*

165 For each plant community, four plots of 20 m x 20 m were established as part of a permanent
166 experimental research site (Gourmelon *et al.* 2016). All plots were separated from each other
167 by at least 100 m. For each plot, plant coverage was assessed using the Braün-Blanquet
168 abundance index (Braun-Blanquet *et al.* 1932). This method measures the percentage of plant
169 coverage by using coefficients ranking from + (representing less than 1% of coverage) to 5

(between 75 and 100% of coverage). Plants were identified mostly at the species level with the support of the IRD Herbarium (Nouméa, New Caledonia). Plant names follow FLORICAL nomenclature (Morat *et al.* 2012). Non-metric multidimensional scaling (NMDS) (Kruskal 1964), conducted on the botanical inventory of each plot, indicated that all four plots from a same plant community were clustered together, allowing us to consider them as replicates for each community type.

1.3. Soil analyses

Soil samples (0 – 15 cm depth) were collected from five different points per plot (supplementary Fig. 1) using a cylindrical core (diameter 8 cm x length 15 cm) and pooled. For each plot, soil texture (sand, silt and clay percentage) was determined using a hydrometer. Soil organic carbon (SOC) was measured in three replicates per plot using a Solid Sample Combustion Unit (SSM – 5000A Shimadzu). Iron and aluminum sesquioxides were measured in three replicates per plot with Inductively Coupled Plasma technology after six extractions following dithionite-citrate system buffered with sodium bicarbonate (Mehra 1958). Cation Exchange Capacity (CEC) was measured with Inductively Coupled Plasma technology after nitrate extraction (Pansu and Gautheyrou 2006).

1.4. Soil aggregate stability tests

To measure soil aggregate stability, the litter and root mat, if present (e.g. in *Nothofagus* rainforests root mats were common), were removed. Soil samples (0 – 15 cm depth) were

191 then collected using a cylindrical core (diameter 8 cm x length 15 cm). To avoid potential
192 spatial heterogeneity, soil was sampled at five points per plot (supplementary Fig. 1). In the
193 field, each soil sample was put into 1 l plastic boxes. Samples were taken back to the laboratory
194 and five samples per plot were pooled to form one composite sample and then air dried for
195 one week. The composite sample was gently sieved to isolate the 3 to 5 mm soil fraction. Soil
196 aggregate stability was measured according to the standardized method NF X 31–515 (Afnor
197 2005) derived from Le Bissonnais (1996a) and Le Bissonnais and Arrouays (1997). We focused
198 on the most disruptive test consisting of quick immersion in water, which induces a slaking
199 action typical of heavy precipitation events. Heavy rainfall events often occur in New
200 Caledonia during the cyclone season (events can comprise more than 400 mm in 6 hours
201 (Météo France 2016a)). After oven drying at 40 °C for 24 h, 10 g of the selected
202 macroaggregates (3–5 mm size fraction) were weighed and then immersed into 50 ml of
203 deionized water for 10 min. Six replicates were examined. Water was then gently discarded
204 and the remaining soil aggregates were transferred onto a 50 µm sieve previously immersed
205 in 95° ethanol to preserve the structure of the soil aggregates. Five helicoïdal movements in
206 two directions were performed manually with constant amplitude (15 cm) and frequency (1
207 cycle s^{-1}). Stable soil aggregates were collected, oven dried at 40°C for 48 h and then gently
208 sieved through a six sieve column (2.00, 1.00, 0.5, 0.2, 0.1 and 0.05 mm) by performing 20
209 identical helicoïdal movements. We then obtained seven diameter classes for the study of
210 stable soil aggregates. Within each of the seven diameter classes (i=1–7), Di [mm] is the mean
211 diameter of each size class. The extreme classes (D1 and D7) are respectively 3.5 and 0.025
212 mm (according to the norm NF X 31–515). The mean weight diameter (MWD in mm) of the
213 soil macroaggregates was calculated as follows:

214 $$MWD = \frac{\sum_{i=1}^{i=7} Mi \; x \; Di}{\sum_{i=1}^{i=7} Mi}$$

215 Mi [g] is the mass of stable soil aggregates isolated within a diameter class. To avoid bias and
216 overestimation of the soil aggregate stability, gravel retained in the 2 mm sieves were
217 collected manually after washing with water and dried at 105°C before weighing. The weight
218 of the fraction retained in the 2 mm sieve (M7) was then corrected by removing the mass of
219 the gravel. In compliance with the norm NF X 31-515, when the percentage of gravel was ≥ 40
220 %, MWD value was not validated.

221

222 *1.5. Data analyses*

223 Based on the species inventory and Braün-Blanquet abundance index, the Bray-Curtis
224 dissimilarity index was calculated and ordinated by non-metric multidimensional scaling
225 (NMDS) to observe dissimilarities of each plant community composition per plot. Additionally,
226 a specific NMDS was done between the sedge-dominated community and *Tristaniopsis glauca*
227 shrubland. To assess the contribution of species to the NMDS, the ENVFIT function of vegan
228 package for R (Oksanen *et al.* 2016) with 999 permutations was computed. We used
229 Permutational Multivariate Analysis of Variance (PERMANOVA) using distance Bray-Curtis
230 matrices to test the hypothesis that species composition and abundance differed between the
231 five plant communities. Differences in soil aggregate stability between plant communities were
232 assessed using Kruskal and Wallis tests, followed by Wilcoxon tests to specify pairwise
233 differences. All statistical analyses were performed using the R 3.3.2 environment for statistical
234 computing (R Core Team 2016).

2. Results

2.1. Plant species inventory

In sedge-dominated community, the plant cover was low (20 %) and vegetation was sparse, with only herbaceous and shrubs present (Table 1). In contrast, in the four other plant communities, the total plant cover was high (≥ 80 %), yet significant differences in the structures of these four communities were noticeable. *Tristaniopsis glauca* shrubland was characterized by the predominance of herbaceous and shrub strata, the absence of tree stratum and consequently a mean height of below 3 m, while the three rainforest types possessed a multi-layer vertical structure with trees, shrubs and herbaceous species. However, the herbaceous stratum in *Arillastrum* rainforest was more developed than in the two other types of rainforest, while the tree cover was less dense.

In terms of species richness, values observed in the sedge-dominated community, *Tristaniopsis glauca* shrubland and *Arillastrum* rainforest were much lower than in the *Nothofagus* rainforest and mixed rainforest (Table 1). Nevertheless, the Simpson index among the five plant communities was comparable (Table 1) and relatively high (around 0.98). The floristic composition and abundance, according to the NMDS (Fig. 3a) and the associated PERMANOVA (Table 2), differed among the five plant communities, except between the *Nothofagus* rainforest and mixed rainforest. The species contributing most to the dissimilarities between the sedge-dominated community and shrubland with *Tristaniopsis glauca* were *Costularia arundinacea* (Cyperaceae), *Garcinia amplexicaulis* (Clusiaceae) and *Myodocarpus fraxinifolius* (Myodocarpaceae) (Fig. 3b).

2.2. Soil characteristics

The soil characteristics were typical of Ferralsols on ultramafic substrates (Table 1). The soil texture (Fig. 4) was overall homogeneous among the different plant communities and mainly classified as silty-clay-loam and clay-loam. One noticeable difference was observed in the *Arillastrum* rainforest which had more sandy soil textures, whilst clay content was comparable among the five plant communities. The SOC percentage (Table 1) increased along the successional gradient from low values (< 1 %) in the sedge-dominated community to high values (> 3.5 %) in rainforests. Similarly, the CEC followed the same trend along the gradient with higher values in rainforests (Table 1). Iron sesquioxides were remarkably high (> 10 %) in soils from all five plant communities (Table 1). In comparison, the content of aluminum sesquioxides was low (< 3 %) (Table 1).

2.3. Soil aggregate stability

In all five plant communities, MWD was above 2 mm which meant that soil aggregates were very stable (Fig. 5). Except for the sedge-dominated community and *Nothofagus* rainforest, remarkably high values of MWD (> 3 mm) were measured in the three other plant communities.

Significant differences in MWD values occurred among the five plant communities ($\chi^2 = 19.25$; *p*-value > 0.001) (Table 3) and MWD values in the sedge-dominated community and *Nothofagus* rainforest were significantly lower (Table 3) compared to MWD in shrubland with *Tristaniopsis glauca* and in mixed rainforest (Fig. 5).

3. Discussion

3.1. High soil aggregate stability in the plant communities investigated on Ferralsols

The soil aggregate stability measured in all five plant communities was high with a MWD above 2 mm, i.e. the aggregates were very stable. This high stability was likely due to the content of iron and aluminum sesquioxides (> 10 %) present in soils. Similar results were found by Oades and Waters (1991) who established that soil aggregates from Ferralsols were stable with regard to rapid wetting: 85 % of the soil material was stabilized in aggregates with a size >0.25 mm and oxides were suggested to be the main stabilizing agents. Sesquioxides of iron and aluminum have also been found to have a positive stabilizing effect on micro-aggregates (Amézketa 1999). Le Bissonnais and Singer (1993) showed in different types of soils that when iron and aluminum sesquioxides were > 2.4 % and organic carbon was > 3 %, neither runoff nor erosion occurred, suggesting that the aggregates were very stable.

The mean MWD measured in the sedge-dominated community was much higher (2.87 mm) than that found in other severely eroded ecosystems, e.g., Mediterranean gully bed ecosystems, where Erktan *et al.* (2016) found a mean MWD of 0.80 mm in the earliest vegetation successional stage. Erktan *et al.* (2016) demonstrated that this stage was characterized by recurrent erosive disturbances limiting plant community development to a dominant herbaceous layer. The difference in results between Erktan *et al's* (2016) study and our own is likely due to the difference in soil characteristics, rather than vegetation or successional stage. The terrain studied by Erktan *et al*. (2016) comprised Jurassic black marls, formed by a mixture of carbonates and clay, whereas the Ferralsols we studied possessed high aggregate stability due to the presence of sesquioxides.

Aggregate stability from vegetation undergoing the second to fifth succession stages possessed MWD values comparable to values found for scrubland and forest in different soil types and climates. For example, Blavet *et al.* (2009) measured a MWD of 3.1 mm in Mediterranean scrubland on Calcic Luvisols and Chenu *et al.* (2000) found a MWD value of 3.19 mm in temperate forests on Vermic Haplubrepts soil. However, it is difficult to compare the effects of vegetation on aggregate stability in different soil types, because the intrinsic characteristics of certain soils e.g., Ferralsols, are the determinant factor driving aggregate stability. Therefore, when aiming to disentangle the relationships between vegetation and aggregate stability, ideally, studies should be carried out on the same type of soil.

3.2. Soil aggregate stability, successional stage and plant communities

Soil aggregate stability increased from early (*i.e.* sedge-dominated community) to the late successional stage (*i.e.* mixed rainforest). Similar trends were observed in sub-arid (Cheng *et al.* 2015; Lin *et al.* 2014), Mediterranean (Erktan *et al.* 2016) and continental climates (Qiu *et al.* 2015). However, the disparity in MWD values observed in the *Nothofagus* rainforest suggest that soil aggregate stability is not only related to the successional stage but also to the composition of the plant community (Fig. 3a). Therefore, a thorough exploration of the abiotic and biotic agents affecting aggregation (e.g. sesquioxides, SOC, plant traits and soil microorganisms), their interactions and feedbacks would be required in different community compositions of the same succession stage.

The greatest increase of MWD (+14 %) was between sedge-dominated community and shrubland with *Tristaniopsis glauca*. There was little difference in MWD values between the

remaining sites (except for *Nothofagus* rainforest). Our results suggest that between the two early stages of succession, a biotic threshold (Hobbs and Harris 2001) was crossed, possibly due to the repeated wildfires (Curt *et al.* 2015) thus limiting the development of the sedge-dominated community to the second stage of succession. The type of restoration response needed depends on which thresholds have been crossed (Hobbs and Harris 2001). Here, the focus should be put on biotic manipulations to restore sedge-dominated community. Increasing plant cover, promoting plant succession and fire protection would be an efficient strategy to stabilize severely eroded ecosystems on Ferralsols in New Caledonia and improve their functionality. Based on the results of the NMDS and the analysis of the floristic dissimilarities between sedge-dominated community and shrubland with *Tristaniopsis glauca* (Fig. 3b), we suggest investigating the contributions of *Costularia arundinacea*, *Garcinia amplexicaulis* and *Myodocarpus fraxinifolius* on the increase in aggregate stability and their influence on the biotic conditions. For example, *Costularia arundinacea* is known to host both plant growth promoting rhizobacteria (PGPR) and arbuscular mycorrhiza (AMF) (Lagrange *et al.* 2011), and the positive influence of mycorrhizal fungi on soil aggregate stability has been well documented (Angers and Caron 1998; Degens 1997; Rillig 2004; Rillig and Mummey 2006; Six *et al.* 2004). For similar reasons, the influence of dominant ectomycorrhizal *Tristaniopsis glauca*, *Arillastrum gummiferum* and *Nothofagus aequilateralis* on soil aggregate stability should also be investigated further.

3.3. Soil aggregate stability and vegetation dynamics

In New Caledonia, wildfires and cyclones are the main disturbances that impact plant succession (Curt *et al.* 2015; Isnard *et al.* 2016; Read and Jaffré 2013). The consequences of such perturbations on aggregate stability must be considered to better understand processes occurring along the successional vegetation gradient. For example, the sedge-dominated community, shrubland with *Tristaniopsis glauca* and *Arillastrum* rainforests, are prone to wildfires and the dynamics of their vegetation relies partially on disturbance by fire (Demenois *et al.* 2017b; McCoy *et al.* 1999). Those processes of ecological succession in ultramafic substrates are very slow. Around 100 years is necessary to establish a shrubland after a fire and the succession between shrubland and rainforest lasts around 250 to 350 years (McCoy *et al.* 1999; Perry and Enright 2002).

Wildfires are a source of heat for iron oxide-rich topsoil, which could lead to changes in the mineralogy of iron oxides (Landers and Gilkes 2007). Dehydroxylation of goethite (α-FeOOH) to hematite (α-Fe_2O_3) occurs after fires in forest or grassland (Grogan *et al.* 2003), leading to a higher content of iron sesquioxides and a subsequently higher aggregate stability in Ferralsols. However, fire will also induce a loss of organic matter in the topsoil (Fox *et al.* 2007). This destruction of organic compounds should decrease aggregate stability, as found in various types of soil (Cerda *et al.* 1995; Oades 1984). Therefore, the consequences of fires on aggregate stability via the production of sesquioxides must be greater than the loss of organic carbon. The net effect of fires probably depends on their frequency and intensity, the initial organic matter content, soil characteristics and the size range of aggregates being considered (Fox *et al.* 2007).

Cyclones are also a major source of disturbance and they open the forest canopy but also disturb the topsoil near the fallen trees. The physical action of uprooting inverts soil horizons

(Beatty and Stone 1986) and creates a pit and mound pattern of micro-relief (Putz 1983). After disturbance, a rapid decomposition of organic matter will occur followed by periods of accumulation (Bormann *et al.* 1995) depending of the frequency of windthrow events, the type and amount of organic matter inputs (Overby *et al.* 2003). As the persistence of monodominant *Nothofagus aequilateralis* rainforests rely on disturbance by cyclones (Demenois *et al.* 2017b), this type of rainforest is prone to such disturbance. Therefore, based on our results, we can assume that cyclones in *Nothofagus* stands will decrease the amount of SOC and as a consequence, aggregate stability.

3.4. Soil aggregate stability and erosion mapping

In our study, we demonstrated that soil aggregate stability on Ferralsols was altered by plant cover, community composition and vegetation dynamics. These new insights could have consequences on erosion mapping in New Caledonia. Ferralsols on ultramafic substrates account for one third of the surface of the archipelago (Fritsch 2012) and erosion mapping is currently based on the Universal Soil Loss Equation (USLE) (Wischmeier and Smith 1978) and Geographic Information Systems (GIS) (Dumas *et al.* 2010; Maurizot and Delfau 1995). Soil aggregate stability is negatively correlated to soil erodibility (Barthès and Roose 2002) which accounts for one factor (K) of USLE. The K factor is calculated through experimental equations and, for a given type of soil, related to the soil texture (clay, silt and sand particle-size classes) and percentage of organic matter (Renard *et al.* 1997). In most types of soil, clay plates and organic matter play a key role in the aggregate organization as major binding agents (Tisdall and Oades 1982). However, if Renard *et al.* (1997)'s equation was applied along our

successional gradient of vegetation, aggregate stability should increase continuously from sedge-dominated community to mixed rainforest. However, such a continuous increase of soil aggregate stability was not observed in our study, suggesting that the K factor on Ferralsols should be different for sedge-dominated community, shrubland with *Tristaniopsis glauca* and even among the different types of rainforests. The high content of iron oxides in Ferralsols which account for > 60 % of the clay particle-size class (Association Française pour l'Etude du Sol 2009) and the particular clay mineralogy in Ferralsols on ultramafic substrate (1:1 ferromagnesian phyllosilicates (Meunier 2005)) might explain this difference, questioning the validity of USLE for erosion mapping in New Caledonia. Additionally, this result may suggest that the K factor, and subsequently soil aggregate stability, is not only related to soil texture and SOC but also to biotic factors such as roots, mycorrhiza, bacteria and their respective exudates (Rillig *et al.* 2015; Six *et al.* 2004; Tisdall and Oades 1982).

Conclusion

We showed that aggregate stability on Ferralsols was high, even for eroded soils. Although the high content of iron sesquioxides could explain such stability, a thorough exploration of the abiotic and biotic agents of aggregation (e.g. sesquioxides, SOC, roots, microorganisms), their interactions and feedbacks is necessary. We also demonstrated that plant communities modify aggregate stability, which mainly increased in the early stages of succession, suggesting that erosion was mainly correlated to plant cover and community composition. We suggest that disturbances (wildfires, cyclones) have consequences on aggregate stability. Repeated wildfires in shrubland with *Tristaniopsis glauca* increased aggregate stability, but

412 constrained the development of plant communities through frequent disturbance. These
413 communities were therefore not able to progress to the next successional stage. In conclusion,
414 we suggest that our results should be taken into account when investigating changes in
415 aggregate stability in a context of ecosystem restoration.

416

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Figure captions

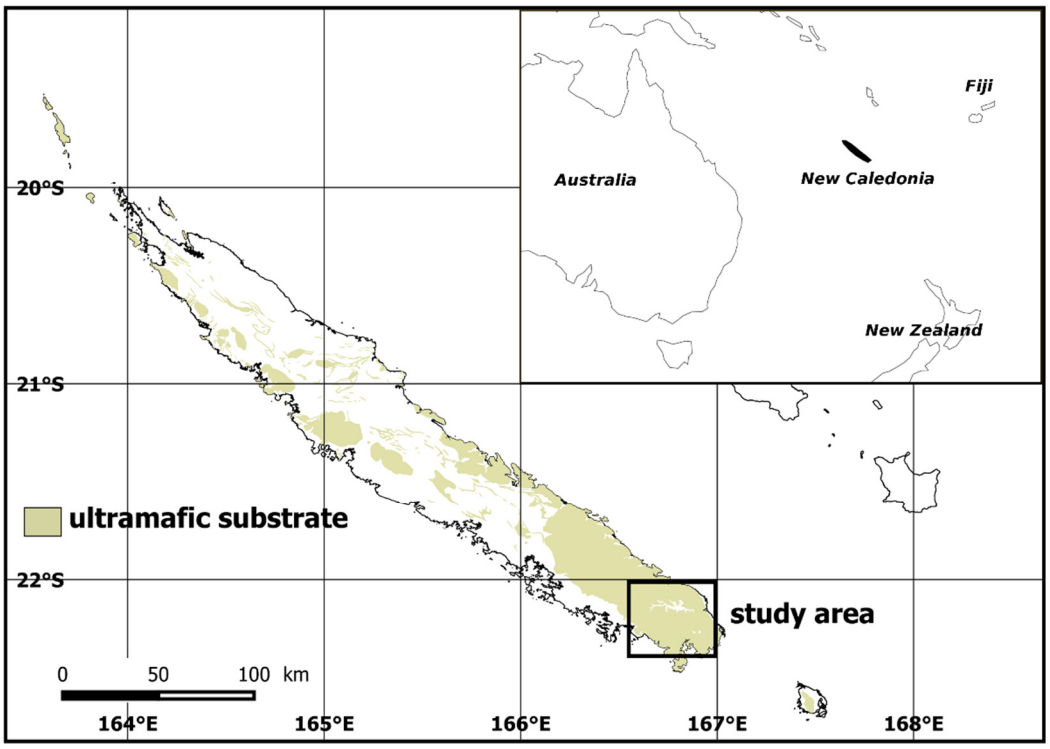
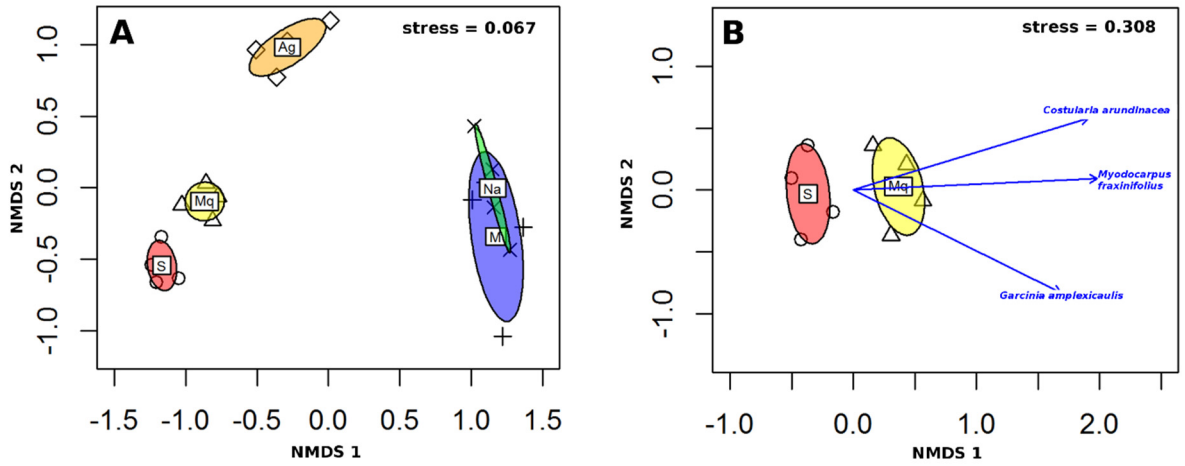


Fig. 1. Location of New Caledonia in the south west Pacific and repartition of ultramafic substrate in the archipelago. The study area is located in the Massif du Grand Sud and is indicated by the square.

Fig. 2. Types of plant communities along the successional vegetation gradient. Images of representative plant communities of each successional stage. a: Sedge-dominated formation; b: shrubland with *Tristaniopsis glauca* (ectomycorrhized); c: *Arillastrum* (ectomycorrhized) forest; d*: Nothofagus* (ectomycorrhized) forest; e: Mixed rainforest.



670

671 **Fig. 3. Non-metric dimensional scaling (NMDS) performed on Bray-Curtis dissimilarity indices for a)**
672 **all five plant communities and b) a focus on sedge-dominated community and shrubland**
673 **dominated by *Tristaniopsis glauca*.** S is Sedge-dominated formation; Mq is shrubland with
674 *Tristaniopsis glauca*; Ag is *Arillastrum* forest; Na is *Nothofagus* forest and M is mixed rainforest.
675 Species contributing most to the dissimilarity between sedge-dominated communities and shrubland
676 with *Tristaniopsis glauca* present are shown with blue arrows ($P \leq 0.01$).

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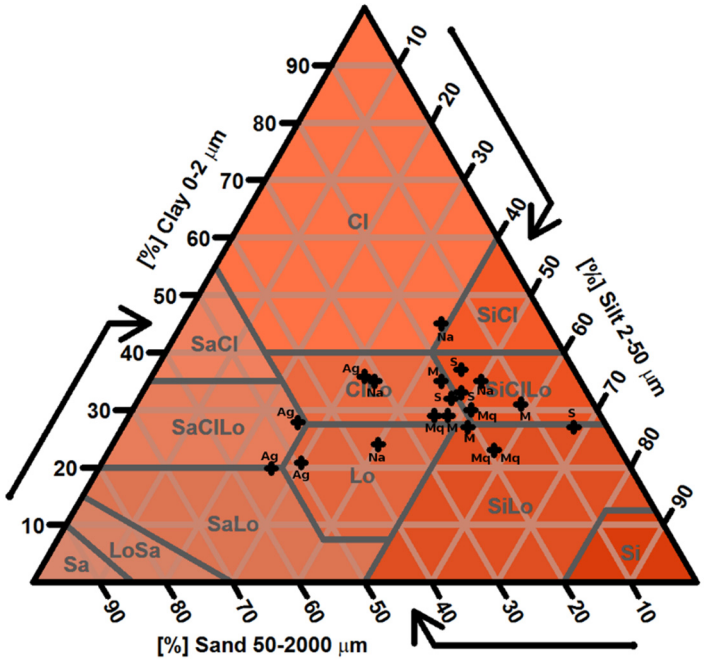
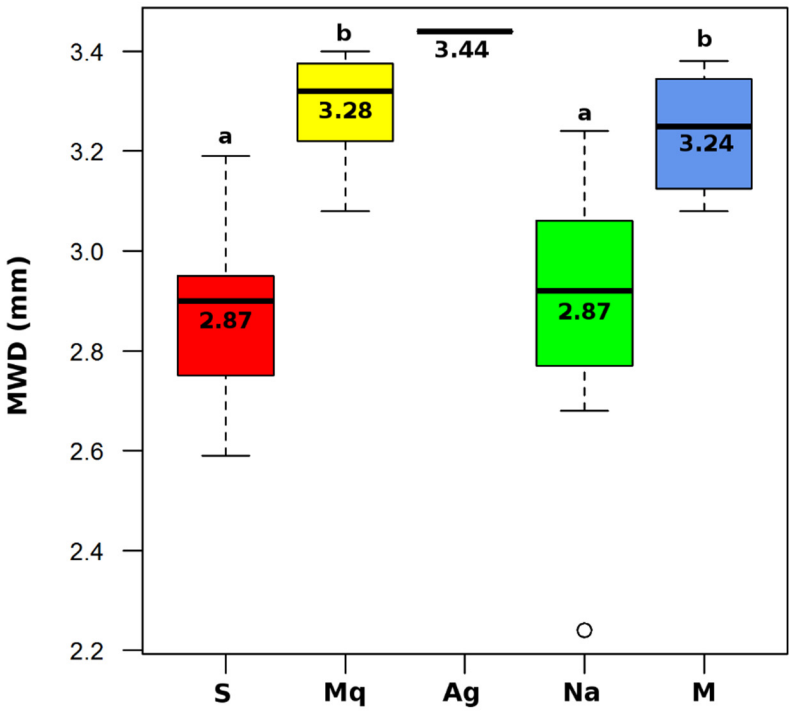


679

680 **Fig. 4. Soil texture triangle in the 20 plots.** Black crosses indicate the values for the plots. S is Sedge-
681 dominated formation; Mq is shrubland with *Tristaniopsis glauca*; Ag is *Arillastrum* forest; Na is
682 *Nothofagus* forest and M is mixed rainforest

683



684

685 **Fig. 5. Soil aggregate stability along the successional gradient.** Mean values are given for each plant
686 community. Letters indicate significant differences between communities given by a pairwise
687 Wilcoxon rank sum test (see Table 3). S is Sedge-dominated formation; Mq is shrubland with
688 *Tristaniopsis glauca*; Ag is *Arillastrum* forest; Na is *Nothofagus* forest and M is mixed rainforest.

689 **Tables**

690 **Table 1. Summary of the vegetation and soil characteristics at each stage of vegetation succession.** Data are means ± standard error; CEC: cation
691 exchange capacity; ECM: ectomycorrhized species; AMF: arbuscular mycorrhized species.

	Sedge-dominated formation	**Shrubland with *Tristaniopsis glauca***	***Arillastrum* forest**	***Nothofagus* forest**	**Mixed rainforest**
Vegetation cover					
Herbaceous	15% ± 4 %	60% ± 14 %	35% ± 17 %	10% ± 8 %	10% ± 7 %
Shrubs	15% ± 5 %	50% ± 8 %	65% ± 14 %	55% ± 5 %	50% ± 8 %
Trees	0%	0%	50% ± 17 %	65% ± 10 %	75% ± 10 %
Total plant cover	20% ± 6 %	80% ± 12 %	85% ± 5 %	80% ± 3 %	90% ± 3 %
Height of the vegetation	< 1 m	2 - 3 m	10 - 15 m	15 - 20 m	15 - 20 m
Species richness	55	76	73	196	171
Simpson index	0,976 ± 0,003	0,978 ± 0,003	0,984 ± 0,003	0,985 ± 0,001	0,983 ± 0,003
Most abundant species					
Herbaceous	*Costularia nervosa (AMF)* *Schoenus neocaledonicus (AMF)*	*Costularia nervosa (AMF)* *Costularia arundinacea (AMF)*	*Costularia arundinacea (AMF)* *Lepidosperma perteres*	*Blechnum chauliodontum*	*Blechnum chauliodontum*
Shrubs	*Tristaniopsis glauca (ECM)* *Pancheria alaternoides (AMF)*	*Tristaniopsis glauca (ECM)* *Sannantha leratii*	*Basselinia deplanchei*	*Deplanchea speciosa*	*Bocquillonia spicata*
Trees	-	-	*Arillastrum gummiferum (ECM)*	*Nothofagus aequilateralis (ECM)*	*Deplanchea speciosa* *Tabernaemontana cerifera*
Texture					
Clay (%)	32.3 ± 4.1	26.3 ± 3.8	26.1 ± 7.4	34.5 ± 8.6	30.5 ± 3.4
Silt (%)	52.3 ± 10.5	53.3 ± 5.9	28.5 ± 3	40.8 ± 6.7	50.5 ± 6
Sand (%)	15.5 ± 7.2	20.5 ± 3	45.5 ± 9.4	24.5 ± 10.6	19 ± 5.4
Soil organic carbon (%)	0.8 ± 0.2	2.6 ± 0.9	3.8 ± 1.2	3.6 ± 1.3	4.9 ± 0.7
Sesquioxides					
Fe (%)	27.4 ± 10.1	29.4 ± 15	38.5 ± 2.3	11.1 ± 4.1	12.6 ± 5.7
Al (%)	2.6 ± 0.4	2.4 ± 0.2	2.3 ± 0.4	1.8 ± 0.8	1.9 ± 0.7
CEC (mval/kg)	47 ± 6	64 ± 6	87 ± 10	122 ± 12	137 ± 31

Data are average value ± standard error for each successional stage (n=4).
ECM : ectomycorrhized species (from Amir and Ducousso (2010))
AMF : arbuscular mycorrhized species (from Amir and Ducousso (2010))

692

693 **Table 2. Results of PERMANOVA on the dissimilarity in floristic composition.**

	Degree of freedom	Sums Of Squares	Mean squares	*F*.model	R^2	P-value
Plant community	4	4.19	1.05	7.26	0.66	***0.001***
Residuals	15	2.16	0.14		0.34	
Total	19	6.35			1	

694

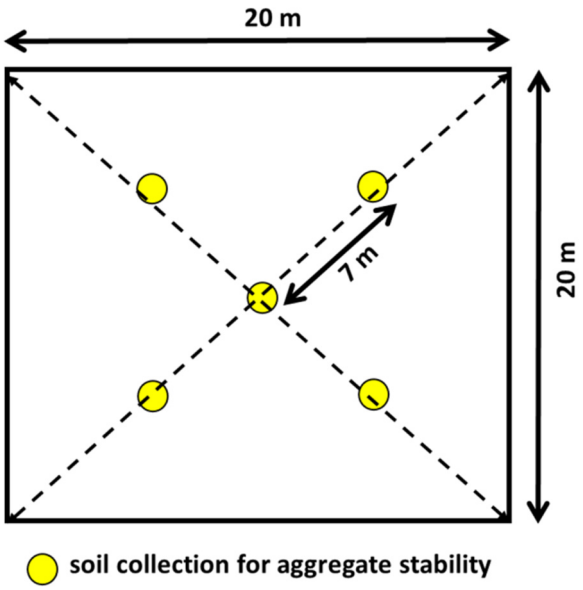
695

696 **Table 3. Statistical tests on soil aggregate stability along the successional gradient.** Kruskal-Wallis and pairwise Wilcoxon rank sum test of soil
697 aggregate stability of the five plant communities. Bold numbers indicate significant p-values.

Aggregate stability ~ plant community	X^2 = 19.253, ***p*-value = 7.008 x 10^{-4}**, df = 4		
	Sedge-dominated formation	**Shrubland with *Tristaniopsis glauca***	***Nothofagus* forest**
Shrubland with *Tristaniopsis glauca*	**0.078**	-	-
***Nothofagus* forest**	1	**0.078**	-
Mixed rainforest	**0.047**	1	**0.078**

698
699

Supplementary material



Supplementary Fig. 1. Sampling design for soil aggregate stability. Core cylinders of soil (8 cm diameter x 15 cm length) were collected at five points: in the center of the plot and diagonally at 7 m from the center.

Linkages between root traits, soil fungi and aggregate stability in tropical plant communities along a successional vegetation gradient

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Abstract

Aims

Determining which abiotic and biotic factors influence soil aggregate stability (MWD) in tropical climates is often confounded by soil type, especially when large amounts of aluminium and iron oxides are present, such as in Ferralsols. We aimed at understanding the role of soil physical and chemical components, vegetation and fungal biomass influencing the aggregate stability of a Ferralsol along a successional gradient of vegetation in New Caledonia.

Methods

Five plant communities, ranging from sedge dominated ecosystems to well-established mixed rainforest were studied. For each community, MWD, soil texture, soil organic carbon (SOC), iron and aluminium sesquioxides, root length density (RLD), specific root length (SRL), root mass density (RMD) and fungal biomass were measured.

Results

Along the successional vegetation gradient, fine roots, RLD and fungal biomass were the main factors having a positive impact on macro-aggregate stability, while SOC and SRL played an indirect but significant role on macro-aggregate stability.

Conclusions

From sedge-dominated community to forest, the increase of above-ground biomass is likely to be the main driver contributing to a higher soil aggregate stability, while among forest types, floristic composition would influence MWD. However, further investigations on soil microbial diversity and biomass should be carried out as microbial interactions with plant communities were too complex to be disentangled in our experiment.

Keywords

Ferralsol, erosion, abiotic factors, biotic factors, ultramafic substrates, New Caledonia

Abbreviations

AMF	Arbuscular mycorrhiza
ECM	Ectomycorrhizal fungi
MWD	Mean weight diameter
PCA	Principal Component Analysis
qPCR	Quantitative PCR
rDNA	Ribosomal DNA
RLD	Root length density
RMD	Root mass density
SRL	Specific root length
SLA	Specific leaf area
SOC	Soil organic carbon

Introduction

Aggregate stability is a key ecosystem process influencing carbon (C) storage (Jastrow *et al.* 1998), nutrient availability (Wang *et al.* 2001) and resistance to erosion (Barthès and Roose 2002). The stabilization of soil aggregates is multifactorial (Amézketa 1999), but is usually related to the quantity and quality of inorganic and organic stabilizing agents (Dalal and Bridge 1996; Lynch and Bragg 1985; Oades 1993). Transient (e.g. organic materials), temporary (e.g. roots, hyphae and bacteria) and persistent (e.g. amorphous iron and aluminum, aromatic humic material, complexes of clay – polyvalent metal – organic matter) also act as binding agents for aggregates (Tisdall & Oades, 1982). However, in certain soils, such as those dominated by iron (Fe) and aluminium (Al) oxides, e.g., tropical Ferralsols, the expression of aggregate hierarchy commonly found in organic soils (Oades and Waters 1991), is perturbed. Tisdall and Oades (1982) suggested that on Ferralsols, the stability of soil aggregates > 2 mm diameter was related to the growth of roots and fungal hyphae, while micro-aggregates (< 250 µm) were stabilized by several mechanisms in which organo-mineral complexes played a dominant role. Until recently, it was thought that aggregate stability in Ferralsols depended more on these organo-mineral complexes than organic matter, but Demenois *et al.* (submitted-b) and Martins *et al.* (2009) , showed that the composition of plant communities influences macro-aggregate stability in Ferralsols, but it is not known what the mechanisms are underlying this relationship.

In their study of aggregate stability in Ferralsols in tropical New Caledonia, Demenois *et al.* (submitted-b) showed that aggregate stability increased from sparse, early successional vegetation to late successional dense, mixed rainforest. Certain plant species had a more pronounced impact on aggregate stability e.g., the sedge *Costularia arundinacea* and the

rainforest trees *Garcinia amplexicaulis* and *Myodocarpus fraxinifolius.* However, it is not known which abiotic and biotic agent(s) of aggregate stability, e.g. Fe and Al oxides, litter, soil organic carbon (SOC), root traits or soil microorganisms, was causing the stabilizing effects observed at the species level. A simultaneous investigation of these various soil and plant characteristics therefore needs performing to elucidate the role of each on aggregate stability in Ferralsols.

The New Caledonia archipelago is currently one of the main producers of nickel in the world (US Geological Survey 2016), and nickel mining is a major cause of soil erosion (Dugain 1953). Soils in the region are also prone to erosion in areas denuded by deforestation and forest fires, especially on ultramafic soils. Apart from providing major nickel reserves, ultramafic substrates in New Caledonia also host a unique terrestrial biodiversity: 96.7 % of the plant species which are endemic to the archipelago, are strictly restricted to ultramafic areas (Isnard *et al.* 2016), highlighting the necessity to preserve and manage soils hosting this unique flora (Isnard *et al.* 2016). Aggregate stability is viewed as a promising indicator of the restoration status of the site in eroded ecosystems (Burri *et al.* 2009). It is therefore vital to better understand the underlying processes of aggregate stability as, in many tropical regions, such as New Caledonia, ecological restoration on eroded sites is a major issue (Losfeld *et al.* 2015).

We focused on a successional gradient of vegetation located in tropical New Caledonia. Five plant communities, representing five phases of vegetation succession, were investigated. We hypothesized that root traits and fungal biomass would explain the differences observed in aggregate stability along the succession gradient, and that the effects of soil organic matter would be masked by the dominant influence of Fe and Al oxides on aggregate stability.

Materials and methods

Study sites

Studies were performed on two field sites located in the Massif du Grand Sud in New Caledonia (Fig. 1). The field sites are part of a permanent experimental research site (Gourmelon *et al.* 2016). The first site, called La Rivière Blanche (22°9'S-166°41'E), is part of the Rivière Bleue Provincial Park. The second site, called Bois du Sud (22°10'S-166°46'E), is part of a botanical reserve created in 2009. The two sites are only eight kilometres apart and are located at an altitude between 300 and 500 m. Mean annual precipitation is 3000 mm and the minimal and maximal mean annual temperatures are 20.5 °C and 26.6 °C (Météo France 2016b). Both sites were selected according to three main criteria: (i) presence of ultramafic substrates characteristic of the Massif du Grand Sud, (ii) a slope < 30° and (iii) plant communities were typical of the ultramafic landscape and represented different successional vegetation stages.

Selection and characterization of plant communities along the successional gradient

We selected five plant communities, representing different phases of vegetation succession. Communities ranged from sedge dominated ecosystems to well-established mixed rainforest. They were composed of:

(i) Sedge dominated communities with dominance of *Costularia nervosa* and *C. arundinacea* (Cyperaceae). In these communities, sedges make up 15 % of ground cover and are considered as an early successional stage (Fig. 2a).

(ii) Open sclerophyllous shrubland dominated by *Tristaniopsis glauca* (Myrtaceae) (Fig. 2b) (Jaffré 1970). *Tristaniopsis glauca* is ubiquitous in shrublands of the Massif du Grand Sud and is associated with ectomycorrhizal fungi (Amir and Ducousso 2010).

(iii) Monodominant *Arillastrum gummiferum* rainforest which could succeed the sclerophyllous shrubland stage (Fig. 2c) (Demenois *et al.* (2017). *Arillastrum gummiferum* usually occurs in extensive, monodominant stands (Sebert 1874; Virot 1956). This species grows exclusively on ultramafic substrates and is associated with ectomycorrhizal fungi (Papineau (1989); Carriconde, unpublished data).

(iv) Monodominant *Nothofagus aequilateralis* rainforest, which is an early successional forest (Fig. 2d) (Read and Jaffré 2013), forming monodominant stands (Read and Hope 1996). *Nothofagus aequilateralis* occurs on ultramafic substrates and is associated with ectomycorrhizal fungi (Carriconde, unpublished data);

(v) Mixed rainforest, which is defined as a forest that is not dominated at its canopy by a single tree species (Fig. 2e). Mixed rainforest is often adjacent to monodominant forest.

For each plant community, four plots of 20 m x 20 m were chosen for soil analyses. All plots were separated from each other by at least 100 m. For each plot, plant coverage was assessed using the Braün-Blanquet abundance index (Braun-Blanquet *et al.* 1932). Plant names follow the FLORICAL nomenclature (Morat *et al.* 2012). Non-metric multidimensional scaling (NMDS) (Kruskal 1964), conducted on the botanical inventory of each plot, indicated

148 that all four plots from a same plant community were clustered together, allowing us to
149 consider them as replicates for each community type (supplementary Fig. 1).

150

151 *Soil aggregate stability measurements*

152 To measure soil aggregate stability, the litter and root mat, if present (e.g. in *Nothofagus*
153 rainforests, root mats were common), were removed. Soil samples (0 – 15 cm depth) were
154 then collected using a cylindrical corer (diameter 8 x length 15 cm). To avoid potential spatial
155 heterogeneity, soil was sampled at five points per plot. In the field, each soil sample was put
156 into 1 l plastic box. Samples were taken back to the laboratory and five samples per plot
157 were pooled to form one composite sample and then air dried for one week. The composite
158 sample was gently sieved to isolate the 3 to 5 mm soil fraction.

159 Soil aggregate stability was measured according to the standardized method NF X 31–515
160 (Afnor 2005) derived from Le Bissonnais (1996) and Le Bissonnais and Arrouays (1997), and
161 is extensively described in Demenois *et al.* (submitted-b). Briefly, we focused on the most
162 disruptive test consisting of quick immersion in water, which induces a slaking action typical
163 of heavy precipitation events. Heavy rainfall events often occur in New Caledonia during the
164 cyclone season (events can comprise more than 400 mm in 6 hours (Météo France 2016a).
165 Six replicates per plot were examined. In compliance with the norm NF X 31-515, when the
166 percentage of gravel was ≥ 40 %, MWD value was not validated and excluded for further
167 analyses.

168

169 *Soil analyses*

For each plot, soil texture (sand, silt and clay percentage) was determined using a hydrometer. Soil organic carbon (SOC) was measured in three replicates per plot using a Solid Sample Combustion Unit (SSM – 5000A Shimadzu). Iron (Fe) and aluminium (Al) sesquioxides were measured on three replicates per plot using Inductively Coupled Plasma technology after six extractions following dithionite-citrate system buffered with sodium bicarbonate (Mehra 1958).

Root trait measurements

For each plot, soil (0 – 15 cm depth) was sampled at five points per plot using a cylindrical corer (diameter 8 x length 15 cm) in order to obtain a soil volume of five cylinders of 754 cm^3 each. To avoid potential spatial heterogeneity, the five samples were pooled to form one composite sample which was then weighed in the laboratory. Three soil subsamples (15 % of fresh weight) of the composite sample were then taken and used as replicates for each plot. Each soil subsample was weighed and roots were extracted from soil by washing them with tap water in a column of two sieves (2.00 and 0.1 mm mesh size). Roots were collected from the two sieves, rinsed and stored in water. To remove impurities, roots were bathed in an ultrasonic bath for 1 min. For each soil subsample, root fresh weight was measured.
For root morphological measurements, one subsample of roots was selected from each soil subsample and weighed (> 25 % of root fresh weight). Thus, three subsamples of roots were used as replicates for each plot. The root fragments were then spread out with no overlapping, in a thin layer of water in a glass container (40 x 30 x 2 cm), and scanned using a flatbed scanner (Epson Expression 10000XL) at a resolution of 600 dpi (Pierret *et al.* 2013). The contrast between roots and background was sufficient for subsequent image

193 segmentation and no dying was necessary. Analyzed roots were then recovered and oven
194 dried at 60 °C during 72 h, and weighed to obtain their dry mass (Pérez-Harguindeguy *et al.*
195 2013). Root images were analyzed with the open source software IJ_Rhizo (Pierret *et al.*
196 (2013), http://www.plant-image-analysis.org). Total root length and the length of roots in
197 254 diameter classes (0.085 mm width from 0 to above 21.5 mm) were measured by the
198 software. Specific root length (SRL) was calculated as the ratio between total root length and
199 dry mass. The percentages of very fine (diameter < 0.2 mm) and fine (0.21 – 1.0 mm) roots
200 were defined as the ratio of length in a given root class to total root length, following the
201 root classification defined by Miller and Jastrow (1990). Total root mass density (RMD) was
202 calculated by the ratio between the total root dry mass and the soil volume from which
203 roots were extracted. The root length density (RLD) was calculated as RLD = SRL x RMD. Total
204 root dry mass was calculated from the total root fresh weight and the humidity percentage
205 of the roots obtained from the dry subsamples.
206

207 *Fungal biomass measurements*

208 A quantitative PCR-based (qPCR) approach was used to assess the abundance of fungi in the
209 soil for each plot (Chemidlin Prévost-Bouré *et al.* 2011; Wallander *et al.* 2013). Fungal
210 biomass is expressed in number of copies of 18S rDNA gene per g of soil. Fifty ml of the
211 collected soil was lyophilised during 48 h then homogenized in a mortar and pestle with
212 liquid nitrogen. Total DNA was extracted from 4 x 0.25 g ground soil subsamples using the
213 Mo Bio PowerSoil DNA extraction kit (MOBIO Laboratories™, USA) (Fierer *et al.* 2012) and
214 then pooled to obtain one soil DNA extract for each plot. FR1 and FF390 primers (Vainio and

215 Hantula 2000) were chosen as they are relevant for a robust and specific detection of the soil
216 fungal community (Chemidlin Prévost-Bouré *et al.* 2011).
217 For each soil DNA extract, the qPCR products were amplified on an ABI PRISM 7300 Real
218 Time PCR System (Applied Biosystems™, France) using SYBR Green as detection system in a
219 reaction mixture of 20 µl containing 1.25 mM of each primer (FR1 and FF390), 10 µl of SYBR
220 Green PCR master mix (Applied Biosystems™, France), including hot-start enzyme AmpliTaq
221 Gold® DNA polymerase, SYBR® Green I dye, dNTP mix (with dUTP), ROX and 5 mM $MgCl_2$,
222 4 µl of template DNA, and DNAse – RNAse-free water to complete the final 20 µl volume.
223 The qPCR conditions were the following: an initial step of 10 min at 95°C for enzyme
224 activation, followed by 45 PCR cycles with 15 s at 95°C for denaturation, 30 s at 52°C for
225 hybridization, and an elongation step of 60 s at 70°C. Data were acquired at the end of this
226 elongation step. A final step was added to obtain a specific denaturation curve. Purity of the
227 amplified products was checked by observation of a single melting peak. Real-time qPCR
228 products obtained from DNA from a pure culture of *Cortinarius sp.* (strain FC12_35_1 from
229 the IAC fungal collection) were cloned in a plasmid (pGEM-T Easy Vector System, Promega,
230 France) and used as standard for the qPCR assay after quantification with a Nanodrop 2000
231 Spectrophotometer (ThermoScientific™, USA). As purified soil DNA extracts may still contain
232 PCR inhibitors, serial dilutions of the DNA templates (1/10 to 1/1000) were used to
233 determine the amount of DNA to be used in the qPCR assay.
234

235 *Data analyses*

Differences in soil parameters (clay, SOC, Fe- and Al-sesquioxides), root traits, fungal hyphae and soil aggregate stability were assessed using Kruskal and Wallis tests, followed by Wilcoxon-Mann-Whitney rank sum tests to specify pairwise differences.

Relationships between soil aggregate stability, root traits, fungi and soil characteristics were investigated *via* a Principal Component Analysis (PCA) for abiotic and biotic factors influenced by plant communities. Correlations were explored with a Spearman correlation test. All statistics analyses were performed using the R.3.3.2 environment for statistical computing (R Core Team 2016).

Results

Soil aggregate stability

In all five plant communities, MWD was above 2 mm which meant that soil aggregates were very stable (Table 1). MWD varied among plant communities as significant differences in MWD values occurred ($\chi^2 = 59.64$; p-value < 0.001, Table 1). Significantly lower values of MWD were measured in the sedge-dominated community and *Nothofagus* rainforest compared to the three other plant communities (Table 1). In contrast, significantly higher values of MWD were measured in the *Arillastrum* forest (Table 1).

Soil characteristics

Clay content was comparable among the five plant communities (Table 1). The SOC content varied significantly among the plant communities ($\chi^2 = 43.29$; p-value < 0.001, Table 1), and increased continuously along the successional gradient from low values in the sedge-

dominated community (7.9 mg.g^{-1} ± 2.4) to high values in rainforests (> 36.2 mg.g^{-1}, Table 1). Fe-sesquioxides were very high (> 100 g.kg^{-1}) in soils from all five plant communities (Table 1), and varied significantly between communities (χ^2 = 12.03; *p*-value < 0.05, Table 1). Two groups were distinguished: (i) sedge-dominated community, shrubland with *T. glauca* and *Arillastrum* forest and (ii) *Nothofagus* forest and mixed rainforest. The former had significantly higher values of Fe-sesquioxides (Table 1). In contrast, the content of Al-sesquioxides was low (< 30 g.kg^{-1}) and no significant differences were found among plant communities (Table 1).

Root traits

Significant differences in specific root traits were found between the five plant communities (Table 1). The sedge-dominated community had significantly lower RLD (37.5 ± 41.5 km m^{-3}), RMD (3 ± 4.8 kg m^{-3}), mean root diameter (0.29 ± 0.13 mm) and percentage of fine roots (44 ± 14 %, Table 1) compared to the other plant communities. In contrast, the sedge-dominated community possessed significantly higher values of SRL (34.8 ± 20.3 m g^{-1}) and percentage of very fine roots (53 ± 18 %, Table 1).

Shrubland with *T. glauca* and *Arillastrum* forest had high RLD (> 180 km m^{-3}) but these values were not significantly different to those for the *Nothofagus* forest and mixed rainforest (110 – 115 km m^{-3}, Table 1). Concomitantly, these four communities had comparably high values of RMD (between 20 and 30 kg m^{-3}) and percentages of fine roots (> 65 %, Table 1). However, in the mixed rainforest and, to a lesser extent, in the *Arillastrum* forest, RMD was significantly greater than in the other communities (> 70 %, Table 1). For SRL, values decreased continuously along the successional gradient from the sedge-dominated community to the rainforest (< 10 m g^{-1}, Table 1).

281

282 *Fungal biomass*

283 Significant differences in fungal biomass were found between plant communities despite a
284 high variability in results (Table 1). Soil in the sedge-dominated community contained a
285 significantly lower average number of copies of 18S rDNA gene per g of soil compared to the
286 other plant communities (Table 1). The values ranged between < 10^3 copies.g^{-1} for the
287 sedge-dominated community, while values > 10^4 copies.g^{-1} for shrubland with *T. glauca* and
288 the different types of rainforests were found (Table 1).

289

290 *Relationships between soil aggregate stability, abiotic and biotic factors*

291 According to the results of the PCA (Fig. 3), positive correlations between MWD, RLD, Fe-
292 sesquioxides (Fe_2O_3), percentage of fine roots (FR) and fungal biomass were expected, while
293 negative correlations between MWD, percentage of very fine roots (VFR) and SRL appeared.
294 The first and second principal components explained respectively 56 % and 17 % of the total
295 variance (Fig. 3). Axis 1 was positively correlated with the percentage of fine roots, root
296 mean diameter, SOC and MWD to a lesser extent and was negatively correlated with the
297 percentage of very fine roots and SRL (Fig. 3). Axis 2 was positively correlated with Fe-
298 sesquioxides, MWD, RLD and fungal biomass (Fig. 3).

299 Significant and positive correlations between MWD and percentage of fine roots, fungal
300 biomass and RLD were found (Fig. 4). Besides, SOC was significantly and positively correlated
301 with percentage of fine roots, fungal biomass and RLD (Fig. 4). In contrast, SRL was
302 significantly and negatively correlated with percentage of fine roots and fungal biomass

303 (Fig. 4). Surprisingly, the expected positive correlation between MWD and Fe-sesquioxides
304 was not found.

305

306 *Soil aggregate stability, abiotic factors, biotic factors and successional gradient*

307 Results showed that the significant increase in MWD between the sedge-dominated
308 community and the shrubland with *T. glauca* was positively correlated to an increase in RLD,
309 percentage of fine roots, fungal biomass and SOC, as well as a decrease in SRL (Fig. 5).
310 Between shrubland with *T. glauca* and *Arillastrum* forest, the increase in MWD was linked to
311 higher SOC (Fig. 5). The decrease in MWD between *Arillastrum* and *Nothofagus* forests was
312 correlated to an increase in the percentage of very fine roots, whereas the higher value of
313 MWD in mixed rainforest was related to a decrease in the percentage of very fine roots and
314 SRL, and an increase of SOC (Fig. 5).

315

316 **Discussion**

317 *Relationships between soil aggregate stability, root traits and fungi*

318 We showed that the influence of plant communities on soil aggregate stability was due to
319 specific root traits and associated fungal communities. Tisdall and Oades (1982) suggested
320 that on Ferralsols, the stability of soil aggregates > 2 mm diameter was related to the growth
321 of roots and fungal hyphae, while micro-aggregates (< 250 µm) were stabilized by several
322 mechanisms in which organo-mineral complexes (e.g. complexes of clay-polyvalent metal-
323 organic matter) played a dominant role. Therefore, our results showed that along the
324 successional gradient of vegetation, the influence of plant communities was mainly on

325 macro-aggregates. In contrast, the binding of micro-aggregates appears to be relatively
326 permanent (Tisdall and Oades 1982), which might explain the absence of correlation
327 between the variations of Fe-sesquioxides along the successional gradient and MWD in our
328 study, where soil contained more than 10 % of sesquioxides.

329 We found that the percentage of fine roots, RLD and fungal biomass were the main biotic
330 factors having a significant and positive impact on aggregate stability. The influence of fine
331 roots on the formation of stable aggregates has already been shown several times (e.g.
332 Gyssels *et al.* 2005; Miller and Jastrow 1990), thus our findings are consistent with these
333 previous studies. Fine roots produce exudates, acting as binding agents, and enmesh and
334 entangle soil particles (Degens *et al.* 1994; Hütsch *et al.* 2002; Six *et al.* 2004). The influence
335 of fine roots on aggregate stability might also be enhanced by indirect mechanisms. For
336 example, fine roots host mycorrhizal fungi that are also able to stabilize soil aggregates
337 directly by mechanical and chemical pathways. Indirectly, mycorrhizas promote root growth
338 and branching, which in turn enhances aggregate stability over time (Rillig and Mummey
339 2006). Fine roots also enrich soil with organic compounds *via* the production of exudates or
340 through decomposition, again stimulating soil microbial communities, which improves
341 aggregate stability (Eisenhauer *et al.* 2010; Jastrow *et al.* 1998).
342 We found a strong correlation between RLD and aggregate stability. Similarly, Gyssels *et al.*
343 (2005) showed that water erosion rates exponentially decreased with increasing root mass.
344 Thus, higher RLD is expected to increase soil aggregate stability (Graf and Frei 2013; Miller
345 and Jastrow 1990; Pérès *et al.* 2013). The main stabilizing effect of the roots is likely through
346 mechanical enmeshment. However, as fungal biomass was also positively correlated to RLD,
347 we could not exclude a stimulating effect of mycorrhizal fungi on root growth (Smith and
348 Read 2010).

349 It is generally recognized that fungi act as key biotic agents in the aggregation and
350 stabilization of aggregates (Oades 1984), which is consistent with our results. In particular,
351 mycorrhizal fungi contribute to stability at different spatial scales directly by charge,
352 adhesive, and enmeshment mechanisms (Graf and Frei 2013). Arbuscular mycorrhizal fungi
353 (AMF) are known to positively influence stability (Bedini *et al.* 2009; Martin *et al.* 2012;
354 Miller and Jastrow 2000; Rillig *et al.* 2002; Ritz and Young 2004; Tisdall and Oades 1982), but
355 the contribution of ectomycorrhizal fungi (ECM) to the formation and stabilization of
356 aggregation has only been demonstrated to a certain extent (Graf and Frei 2013; Thornton
357 *et al.* 1956). In a previous study, Demenois *et al.* (submitted-b) showed that *Costularia*
358 *arundinacea*, an AMF host plant, explained most of the floristic dissimilarity between the
359 sedge-dominated community and the shrubland with *T. glauca*. Similarly, the dominant ECM
360 host plants *Arillastrum gummiferum* and *Nothofagus aequilateralis* were responsible of the
361 floristic dissimilarities between *Arillastrum, Nothofagus* and mixed rainforests, the
362 (Demenois *et al.* 2017). We could therefore hypothesize that AMF and specific root traits
363 contributed synergistically to the higher aggregate stability between sedge-dominated
364 community and shrubland with *T. glauca*, while the influence of ECM association remains
365 unclear. However, the qPCR based approach does not allow us to distinguish between AMF
366 and ECM. It is known that microbial richness, composition and abundance are linked to the
367 dominant species in a plant community (Gourmelon *et al.* 2016), therefore, fungal diversity
368 should be explored further to elucidate the influence of AMF and ECM on aggregate stability.
369

370 *Soil aggregate stability along the successional gradient of vegetation*

371 Soil aggregate stability increased from early (*i.e.* sedge-dominated community) to the late
372 successional stage (*i.e.* mixed rainforest, Fig. 5.). The sedge-dominated community was

373 characterized by a low plant cover (around 15 %), low SOC (< 1 %), lower RLD and
374 percentage of fine roots compared to the other plant communities, a small fungal biomass
375 and a higher SRL. These factors resulted in poorer aggregate stability in the sedge-
376 dominated community in comparison to the other successional stages (Fig. 5). The increase
377 of plant cover and the development from the sedge-dominated community to the
378 *Arillastrum* forest also increased aboveground biomass. Carbon input to soil from increased
379 litter and woody debris would therefore also be amplified in forests, improving aggregate
380 stability.

381 Between the different forest types, our results indicated a complex pattern. We found that
382 despite comparable values of plant cover (around 80 %), SOC (> 3 %), RLD and fungal
383 biomass between the three communities, soil aggregate stability in the *Nothofagus* forest
384 was significantly lower than that of the other forest types and surprisingly similar to that
385 found in the sedge-dominated community. Only the percentages of fine (decreased) and
386 very fine roots (increased) were significantly different in the *Nothofagus* forest compared to
387 the other types of forest. The higher percentage of very fine roots in the *Nothofagus* forest
388 might be related to the presence of a root mat which is specific to this type of rainforest. The
389 negative linkage between the percentage of very fine roots and aggregate stability was also
390 found by Erktan *et al.* (2016) on Jurassic black marls in a Mediterranean climate, but the
391 underlying mechanism remains unclear.

392 Apart from different root traits, *Nothofagus* forests are characterized by specific microbial
393 (fungi, bacteria) richness, composition and abundance (Gourmelon *et al.* 2016). Such an
394 effect of plant formation on microbial communities may be notably due to host preference,
395 litter quality and root exudates (Dickie 2007; Gourmelon et al. 2016; Sourkova *et al.* 2005).

The impact of fungal specificity and host plant on aggregate stability was already shown, at least for AMF (Kohler *et al.* 2016). Thus, the influence of different soil micro-organisms communities on aggregate stability could not be excluded as it can result in variable inputs of above- and below-ground organic matter into soil (Kohler *et al.* 2016), and therefore be related to SOC. At this stage, we can only suggest that floristic composition is the main driver of aggregate stability between forest types but further work is required to elucidate the effects of soil microbial communities associated to both leaf litter and roots in these different forest types.

Conclusion

We showed that in a Ferralsol on an ultramafic substrate, plant community type positively influenced macro-aggregate stability, due to interactions with root traits and associated fungal communities. Micro-aggregate stability was not significantly different between communities and was likely more influenced by the intrinsic nature of the Ferralsol. Fine roots, RLD and fungal biomass were the main factors having a positive impact on macro-aggregate stability.

We suggest that from sedge dominated community to forest, the increase of aboveground biomass contributes more to aggregate stability because of the higher input of carbon to soil from forest litter. Between different forest types, the floristic composition influenced aggregate stability, through differences in root traits and fungal communities. However, further investigations on soil microbial communities should be carried out as their interactions with different types of plant communities were too complex for us to reach broad conclusions.

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Figure captions

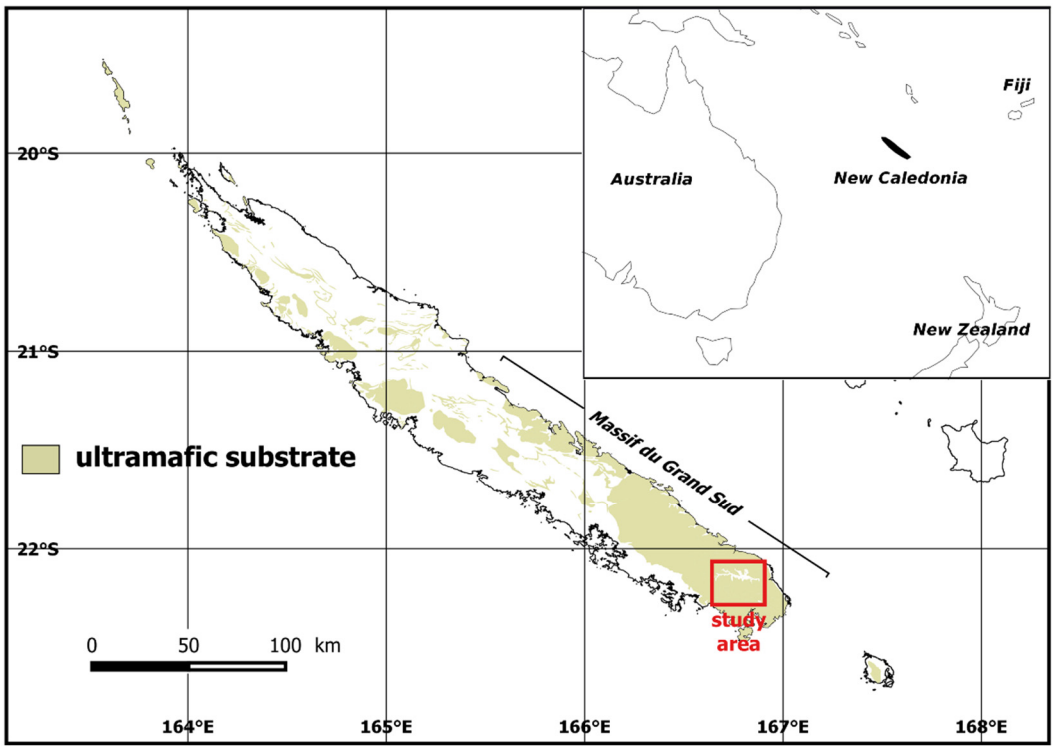
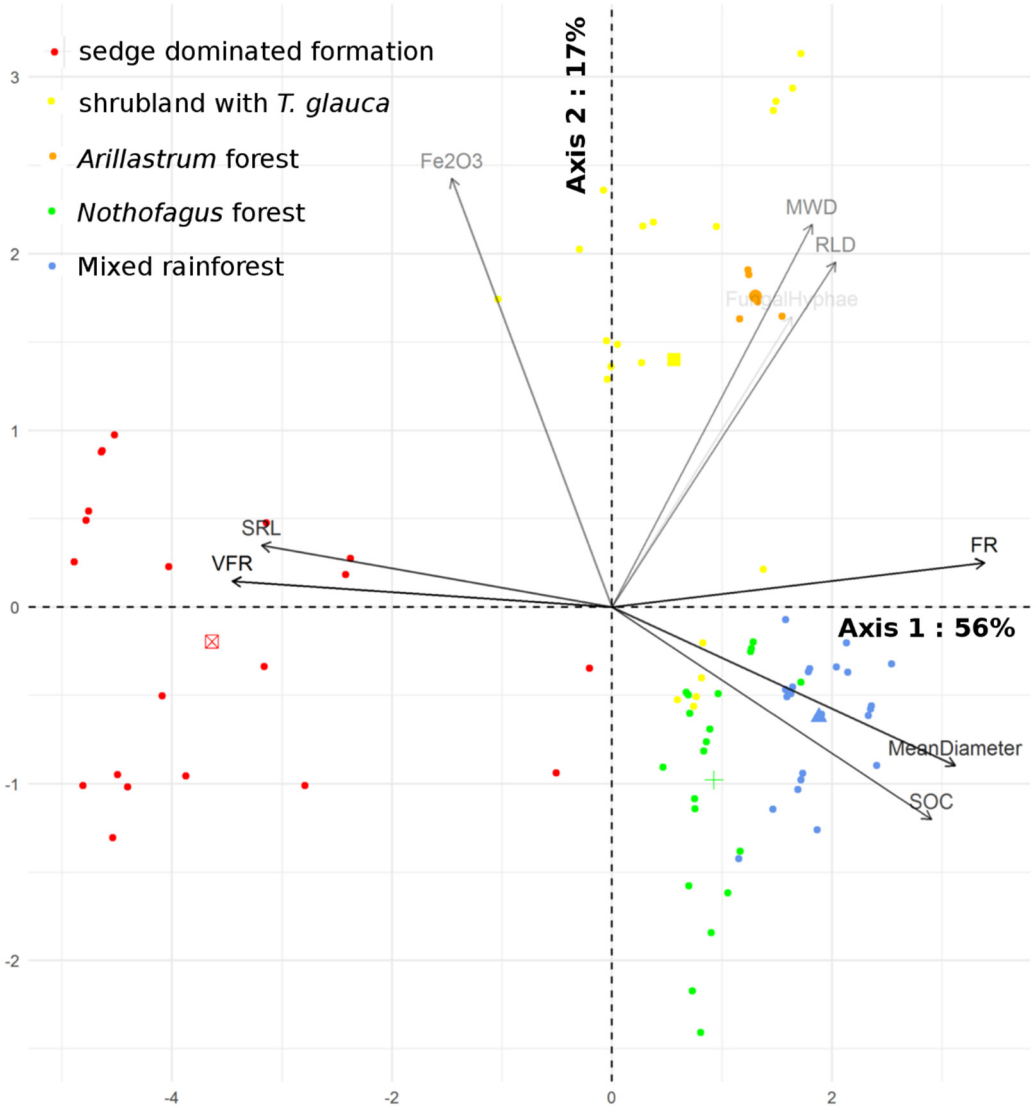


Fig. 1. Location of New Caledonia in the south west Pacific and distribution of ultramafic substrate in the archipelago. The study area is located in the Massif du Grand Sud and is indicated by the red square.

Fig. 2. Types of plant communities along the successional vegetation gradient. Images represent the different plant communities of each successional stage. a) Sedge-dominated community; b) shrubland with *Tristaniopsis glauca* (ectomycorrhizal); c) *Arillastrum* (ectomycorrhizal) forest; d) *Nothofagus* (ectomycorrhizal) forest; e) mixed rainforest.



645

646 **Fig. 3. Principal component analysis of soil, root characteristics and fungal biomass along the**
647 **successional gradient.** Larger symbols indicate the center of each plant community. Cos^2 for
648 variables are shown via the colour scale: light grey <0.5; grey 0.5< < 0.8; black >0.8. Abbreviations
649 are: MWD: mean weight diameter; RLD: root length density; SOC: soil organic carbon; SRL: specific
650 root length; FR: % of fine roots; VFR: % of very fine roots

651

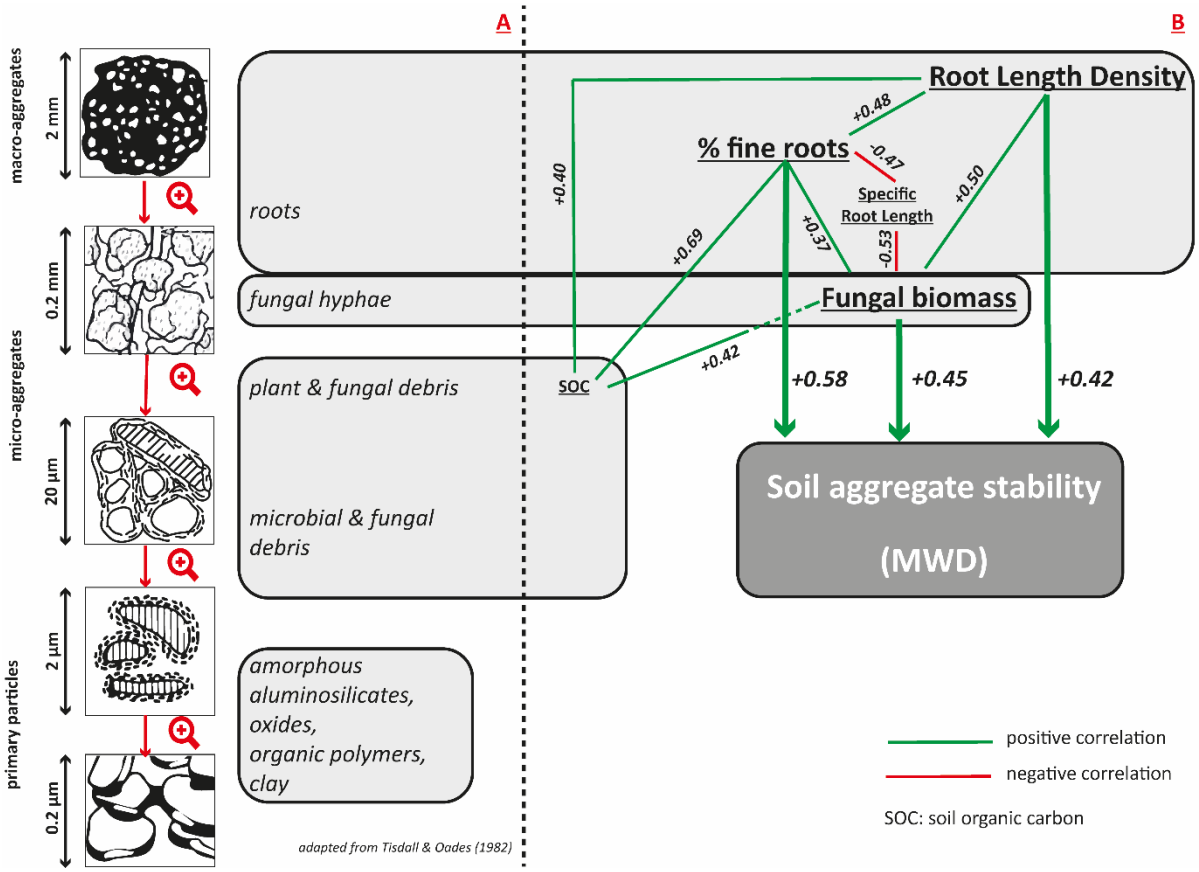


Fig. 4. A. Model of aggregate organization. Major binding agents are indicated in italics (adapted from Tisdall & Oades (1982)) **- B. Spearman correlations between soil aggregate stability (MWD), soil characteristics, root traits and fungal hyphae along the plant successional gradient.** Only correlations with $P<0.001$ are shown. Indicated values are for ρ. Green lines indicate a positive correlation and red lines a negative correlation. Arrows are for direct linkage with MWD.

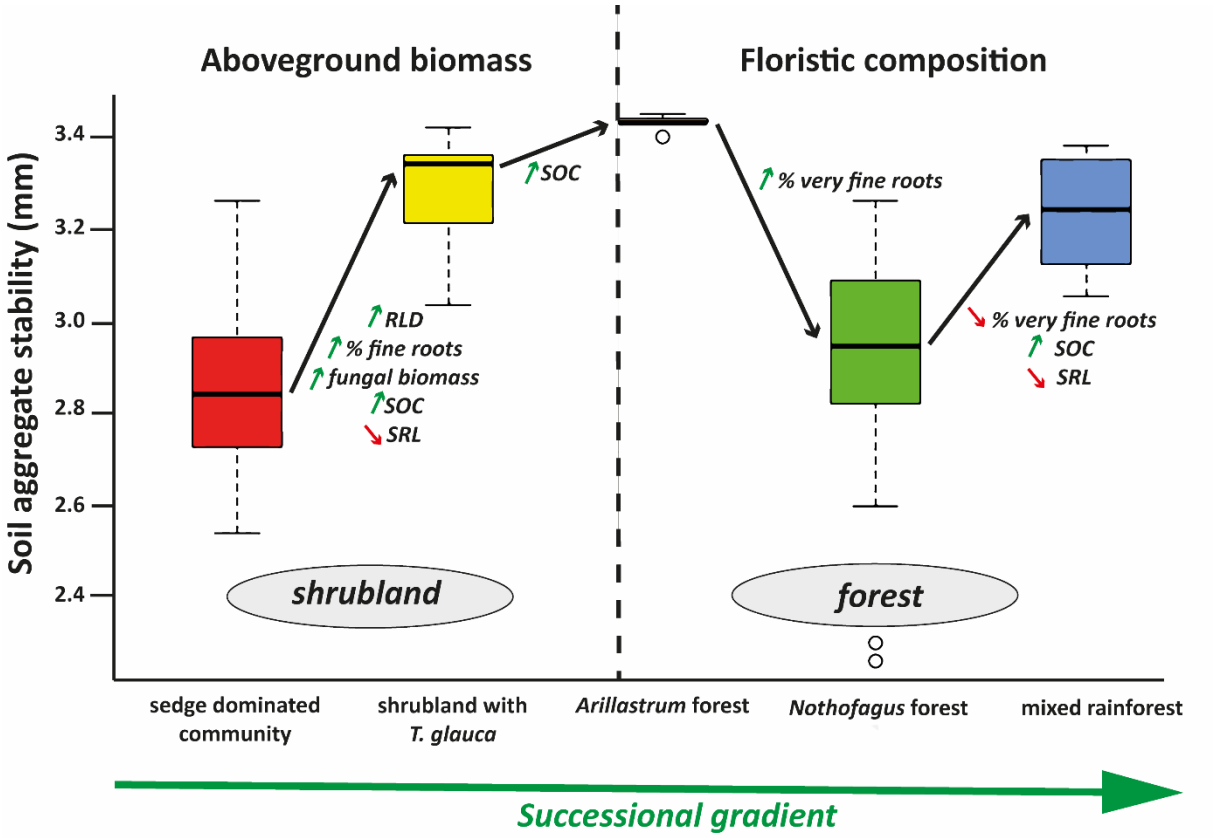


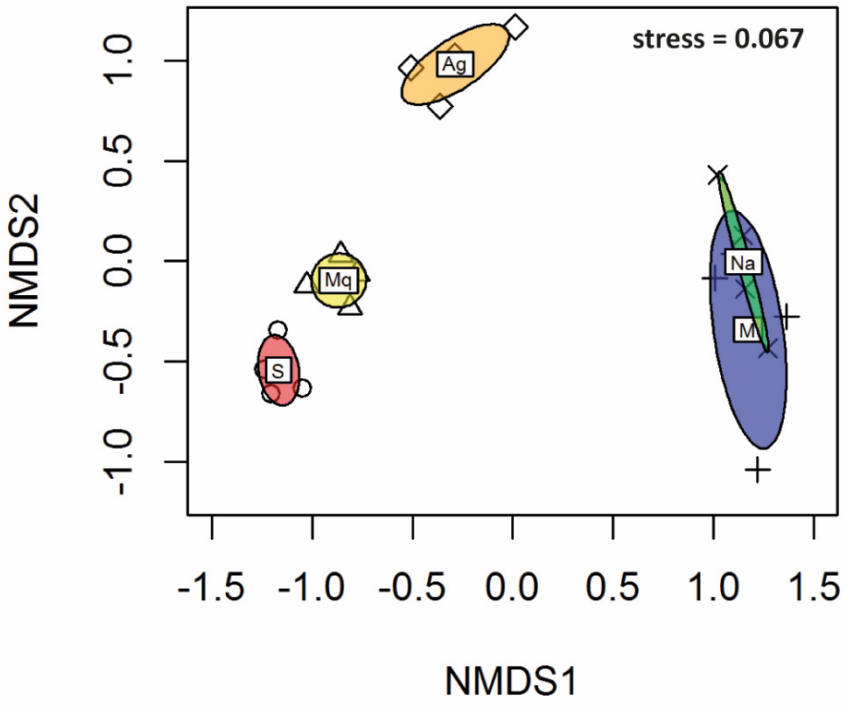
Fig. 5. Soil aggregate stability along the successional gradient. Significant differences in biotic and abiotic factors between the successional stages are shown. Green arrows indicate an increase of the parameter between two successional stages. Red arrows indicate a decrease of the parameter between two successional stages. Outliers of boxplots are represented by white dots.

Tables

Table 1. Statistical tests on soil, roots and fungi characteristics along the successional gradient. Data are means ± standard error for each successional stage. Significant differences between plant communities are indicated by a Kruskal-Wallis test (X^2/*P*). Levels of significance are n.s.: non-significant; *: *P*<0.05; **: *P*<0.01; ***: *P*<0.001. Letters indicate significant differences between plant communities given by pairwise Wilcoxon-Mann-Whitney rank sum test for *P*<0.05.

Variable (Abb./unit)	Sedge dominated formation	Shrubland *with Tristaniopsis glauca*	*Arillastrum* forest	*Nothofagus* forest	Mixed rainforest	Kruskal-Wallis test (X^2/*P*)
Soil characteristics						
soil aggregate stability (MWD / mm)	2.85 ± 0.19 a	3.28 ± 0.11 b	3.43 ± 0.02 c	2.90 ± 0.28 a	3.24 ± 0.12 b	59.64/***
clay (%)	32.3 ± 4.1	26.3 ± 3.8	26.3 ± 7.4	34.8 ± 8.6	30.5 ± 3.4	5.16/n.s.
soil organic carbon (SOC / $mg.g^{-1}$)	7.9 ± 2.4 a	26.1 ± 8.9 b	38.0 ± 11.5 c	36.2 ± 12.8 c	49.3 ± 6.6 d	43.29/***
Fe-sesquioxides (Fe_2O_3 / $g.kg^{-1}$)	273.5 ± 100.5 a	294.2 ± 150.1 a	385.2 ± 23.5 a	111 ± 40.9 b	126.2 ± 57 b	12.03/*
Al-sesquioxides (Al_2O_3 / $g.kg^{-1}$)	26.2 ± 3.6	23.7 ± 2.3	22.8 ± 4.3	18.3 ± 7.8	18.9 ± 7.4	3.61/n.s.
Root characteristics						
Root length density (RLD / $km.m^{-3}$)	37.5 ± 41.5 a	182.6 ± 93.6 b	181.5 ± 73.0 b	115.2 ± 52.2 b	110.8 ± 43.2 b	28.78/***
Root mass density (RMD / $kg.m^{-3}$)	3.0 ± 4.8 a	19.7 ± 8.8 b	29.0 ± 12.2 b	21.5 ± 8.3 b	26.6 ± 7.8 b	32.78/***
Specific root length (SRL / $m.g^{-1}$)	34.8 ± 20.3 a	10.2 ± 5.4 b	6.7 ± 2.6 bc	5.6 ± 2.0 bc	4.5 ± 1.9 c	28.98/***
Mean root diameter (mm)	0.29 ± 0.13 a	0.47 ± 0.07 b	0.62 ± 0.08 c	0.64 ± 0.09 c	0.67 ± 0.07 c	38.86/***
Fine roots (0.2< <1 mm) (%)	44 ± 14 a	69 ± 4 b	71 ± 4 bc	66 ± 4 b	73 ± 5 c	28.64/***
Very fine roots (<0.2 mm) (%)	53 ± 18 a	24 ± 5 b	16 ± 2 c	20 ± 4 d	14 ± 5 c	35.35/***
Fungal characteristics						
fungal biomass (10^3 18S rDNA gene copy number.g_{soil}^{-1})	0.59 ± 0.48 a	18.14 ± 21.36 b	12.86 ± 7.35 b	12.37 ± 11.16 b	10.59 ± 6.20 b	26.88/***

672 **Supplementary material**



673

674 **Supplementary Fig. 1. Non-metric dimensional scaling (NMDS) performed on Bray-Curtis**
675 **dissimilarity indices for the five plant communities.** S is Sedge-dominated formation; Mq is
676 shrubland with *Tristaniopsis glauca*; Ag is *Arillastrum* forest; Na is *Nothofagus* forest and M is mixed
677 rainforest.

Chapitre 4 – Des communautés aux espèces végétales, quelles espèces-outils potentielles pour accroître la stabilité des agrégats des Ferralsols sur substrats ultramafiques ?

Ce chapitre a donné lieu à la soumission de deux articles, respectivement dans les revues *Geoderma* et *Pedobiologia* :

- Demenois J., Carriconde F., Bonaventure P., Maeght J.-L., Stokes A., Rey F., *Impact of plant root functional traits and associated mycorrhizas on the aggregate stability of a tropical Ferralsol,* soumis à Geoderma.
- Demenois J., Rey F., Stokes A., Carriconde F., *Does arbuscular and ectomycorrhizal fungal inoculation improve soil aggregate stability? A case study on three tropical species growing in ultramafic Ferralsols,* accepté dans Pedobiologia.

La finalité de ce travail était d'une part d'évaluer la capacité d'espèces végétales, associées à des champignons mycorhiziens, d'accroître la stabilité des agrégats des Ferralsols sur substrats ultramafiques, et d'autre part d'identifier les traits racinaires et les associations mycorhiziennes contribuant à cet accroissement. Pour ce faire, nous nous sommes intéressés à trois espèces végétales, potentielles espèces-outils pour augmenter la stabilité des agrégats : *Costularia arundinacea*, *Tristaniopsis glauca* et *Arillastrum gummiferum*. Leurs potentialités respectives s'appuient sur les résultats issus de l'approche à l'échelle des communautés (Chapitre 3) ainsi que sur leur caractère dominant et leur statut mycorhizien (AMF et ECM). Par ailleurs, ces trois espèces héliophiles sont couramment utilisées dans les opérations de restauration écologique sur les substrats ultramafiques de l'archipel. Afin de distinguer autant que possible l'effet des traits racinaires et celui des symbioses mycorhiziennes, deux expérimentations complémentaires ont été menées :

- des mesures *in situ* sur des plantes isolées permettant d'étudier en conditions naturelles les effets combinés des traits racinaires et des communautés fongiques ;
- des essais en serre avec ou sans inoculation de champignon permettant d'évaluer respectivement les effets des traits racinaires et des symbioses mycorhiziennes.

Enfin, d'un point de vue technique, l'objectif de la seconde expérimentation était également de réaliser pour la première fois une inoculation contrôlée sur *T. glauca* et *A. gummiferum* à l'aide d'une souche isolée à partir d'un carpophore d'un champignon ECM issu de Ferralsols sur substrats ultramafiques, et ainsi d'en poser les bases techniques, d'en évaluer les effets sur la croissance des plants et *in fine* la faisabilité. Pour mémoire, sur substrats ultramafiques, le rôle fonctionnel des

symbioses mycorhiziennes au sein des formations végétales serait fondamental et permettrait de faire face aux conditions édaphiques extrêmes (Alexander *et al.* 2007; Branco 2010; Schechter and Bruns 2008).

Ainsi, les objectifs scientifiques de ce travail étaient doubles :

- étudier, à l'échelle espèce, en conditions *in situ*, comment les traits racinaires et les communautés fongiques associées influencent la stabilité des agrégats des Ferralsols sur substrats ultramafiques ;
- évaluer l'effet de l'inoculation avec des champignons AMF et ECM sur la stabilité des agrégats des Ferralsols sur substrats ultramafiques.

Les principaux résultats de ce travail sont les suivants :

- *in situ*, seule *C. arundinacea* permet d'augmenter la stabilité des agrégats des Ferralsols sur substrats ultramafiques. En comparaison, des plants isolés de *T. glauca* et d'*A. gummiferum* ne permettraient pas d'accroître la stabilité des agrégats ;
- *in situ*, la masse de racine par unité de volume (Root Mass Density), les racines fines et la longueur de racine par unité de volume (Root Length Density) ont un impact direct et positif sur la stabilité des agrégats, tandis que l'effet positif des champignons AMF est suspecté ;
- les essais en serre confirment que la longueur de racine par unité de volume (Root Length Density) contribue significativement à l'augmentation de la stabilité des agrégats des Ferralsols sur substrats ultramafiques ;
- les essais en serre mettent en évidence l'effet positif des AMF sur la stabilité des agrégats ;
- l'inoculation contrôlée avec *Pisolithus microcarpus* (champignon ECM) permet d'augmenter la stabilité des agrégats des Ferralsols sur substrats ultramafiques.

Ce travail a ainsi permis de mettre en évidence que la combinaison Root Mass Density – Root Length Density – racines fines, avec des valeurs élevées pour ces trois traits racinaires, est efficace pour augmenter la stabilité des agrégats des Ferralsols sur substrats ultramafiques. Par ailleurs, l'efficacité de cette combinaison de traits racinaires est accrue par les symbioses mycorhiziennes (AMF et ECM). Ainsi, des trois espèces végétales évaluées, *C. arundinacea* serait l'espèce-outil la plus efficace pour accroître la stabilité des agrégats des Ferralsols sur substrats ultramafiques. Par ailleurs, l'inoculation contrôlée de *Tristaniopsis glauca* avec *Pisolithus microcarpus* s'est avérée fonctionnelle et efficace pour faciliter la croissance de la plante et stabiliser le sol.

Impact of plant root functional traits and associated mycorrhizas on the aggregate stability of a tropical Ferralsol

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Abstract

In many tropical regions, such as New Caledonia, soil erosion from anthropogenic activities and subsequent ecological restoration are major issues that require detailed soil and vegetation data for the production of management plans. To determine if some plant species are more useful for stabilizing soil aggregates and thus reducing erodibility, we examined three species endemic to New Caledonia, and measured how root traits and associated mycorrhizas influenced Ferralsol aggregate stability. We examined three species that are hosts to different types of mycorrhizas, (i) the sedge *Costularia arundinacea* (Sol. Ex Vahl) Kük., an AMF (arbuscular mycorrhizal fungi) host, (ii) the shrub *Tristaniopsis glauca* Brongn. & Gris and (iii) the tree *Arillastrum gummiferum* (Pancher ex Brongn. & Gris) Baill., both of the latter are ectomycorrhizal fungi (ECM) hosts. Fungal biomass, aggregate stability, soil organic carbon (SOC), iron (Fe) and aluminium (Al) sesquioxides were measured in the soil beneath 20 individuals for each species, as well as in 20 control samples of bare soil. Root functional traits including root mass density (RMD), root length density (RLD) and percentage of fine roots were measured on all individuals. Aggregate stability was very high in all soil samples, likely due to the considerable presence of sesquioxides which may have masked some of the effects of vegetation and mycorrhizas. Nevertheless, aggregate stability was significantly greater in soil beneath *C. arundinacea*, compared to soil from the other two species, which were not significantly different to the control. SOC was significantly higher in soil from beneath all plant species compared to the control. *C. arundinacea* had higher RMD, RLD, percentage of fine roots and fungal biomass compared to the other two species. In conclusion, ECM-hosts had little effect on Ferralsol aggregate stability compared to the AMF-host species. However, C. *arundinacea* also possessed root functional traits that may have

enhanced aggregate stability, regardless of mycorrhiza type. In a wider context, when compared to similar studies, results indicate that aggregate stability measurements on isolated individuals cannot be scaled up to the plant community level.

Keywords

Belowground traits, mycorrhizal symbiosis, plant diversity, erosion, ultramafic substrates, New Caledonia

Highlights

- Aggregate stability of tropical Ferralsols was significantly improved in soils beneath the sedge *Costularia arundinacea* (arbuscular mycorrhizal-host)
- The Ferralsol possessed considerable amounts of sesquioxides which likely masked any effects of ECM on aggregate stability
- High RMD, RLD, percentage of fine roots, AMF fungal biomass and SOC significantly improved Ferralsol aggregate stability

1. Introduction

Soil aggregate stability influences a wide range of physical and biogeochemical processes in the natural environment (Amézketa 1999). The stability of the aggregates and the pores between them affects the movement and storage of water, aeration, biological activity, the growth of plants and erosion (Amézketa 1999). By controlling soil porosity, aggregates enhance water infiltration and water holding capacity (Jastrow *et al.* 1998). Aggregates not only physically protect the soil organic matter that helps bind aggregates together, but also influence microbial community structure (Hattori 1988) and determine nutrient adsorption and desorption (Linquist *et al.* 1997). Therefore, soil aggregate stability contributes to conserve soil fertility (Elliott 1986). Stable soil aggregates are also more resistant to detachment and loss through erosion (Barthès and Roose 2002; Pierson and Mulla 1990). Thus, maintaining high soil aggregate stability is essential for preserving soil productivity and minimizing soil erosion (Amézketa 1999), yet, remains a poorly understood process, especially in a tropical context.

In many tropical regions, such as New Caledonia, an archipelago in the south west Pacific ocean, ecological restoration is a major issue, especially on heavily eroded sites (Losfeld *et al.* 2015). New Caledonia is a hotspot of biodiversity (Myers *et al.* 2000). Apart from providing major nickel reserves, ultramafic substrates in New Caledonia also host a unique terrestrial biodiversity. Over 1200 plant species, 97 % of which are endemic to New Caledonia, are ultramafic-obligate (Isnard *et al.* 2016), highlighting the necessity to preserve and manage soils hosting this unique flora. Demenois *et al.* (submitted-c) showed that in a Ferralsol on an ultramafic substrate, macro-aggregate stability (> 250 µm) was influenced by the floristic composition of plant communities due to interactions with fine root traits (*e.g.*

percentage of fine roots and root length density) and associated fungal communities. However, micro-aggregate stability (20-250 µm) was more likely influenced by the intrinsic nature of the Ferralsol, and especially the high content of iron sesquioxides.

The positive effect of fine roots on soil aggregate stability consists of i) enmeshing fine particles into stable macro-aggregates; ii) drying the localized soil environment around the roots, iii) drawing soil particles together; iv) supplying decomposable organic residues; v) supporting a large microbial population in the rhizosphere; vi) providing food for soil animals and iv) releasing polyvalent cations (Pojasok and Kay 1990). However, the effect of fine roots on soil aggregate stability is variable and depends largely on soil type (Le Bissonnais *et al.* submitted): differences in fine root quantity and architecture will determine the overall influence of root penetration on aggregates (Carter *et al.* 1994); root exudation is variable among plant species (Haynes and Beare 1997; Hütsch *et al.* 2002) and decomposition of dead roots is related to the amount and the decomposability of root material (Robinson and Jacques 1958). In a comparative study of the effects of fine roots versus soil characteristics, Le Bissonnais *et al.* (submitted) showed that between sites, soil chemical properties and organic carbon content were the main drivers of stability, but that within a site, plant fine root traits, and in particular root biomass and root length density, influenced most aggregate stability. Similarly, plant species diversity and richness have been demonstrated to promote the formation and the stabilization of soil aggregates (Erktan *et al.* 2016; Pérès *et al.* 2013; Pohl *et al.* 2009), largely due to a more optimal temporal and spatial occupation of roots in the soil matrix. However, these studies did not take into account the type of mycorrhizas associated with the plant communities.

Fungal transformants and exudates act by coating fine soil particles with a layer of organic matter and by adhering the particles embedded and held on the surface, forming micro-aggregates. Like, plant roots, fungal hyphae can bind and enmesh micro-aggregates into macro-aggregates (> 250 µm) (Graf and Frei 2013; Tisdall 1994). Mycorrhizal fungi also indirectly affect aggregate stability through their host plants, particularly by accelerating the development of their root network and by serving as a distribution vector for associated micro-organisms (Graf and Frei 2013). Although the influence of arbuscular mycorrhiza (AMF) on aggregate stability has been demonstrated several times (Miller and Jastrow 2000; Rillig 2004; Wilson *et al.* 2009), the contribution of ectomycorrhizas (ECM) to the formation and stabilization of soil aggregates has not been elaborated in detail. ECM are usually more host-specific than AMF and are generally associated with woody species (Wang and Qiu 2006). Studies that comprehensively describe the influence of ECM characteristics on aggregate stability (e.g. filamentous growth, mycelial networks that stretch beyond the rhizosphere and the production of polysaccharides and hydrophobines), are scanty (Caesar-Ton That *et al.* 2001; Graf and Frei 2013; Tagu *et al.* 2001).

To determine if some plant species and their associated mycorrhizas are more useful for stabilizing soil aggregates, we examined bare soil and three plant species endemic to New Caledonia, and measured how root traits and mycorrhizas influenced Ferralsol aggregate stability. Plant species comprised herbaceous and woody species and were host to either AMF or ECM. We hypothesized that at the species level, an herbaceous species (AMF-host) would have a greater effect than woody species, because of the large quantity of fine roots present, which would also increase AMF biomass. As woody species have a lower quantity of fine roots (Le Bissonnais *et al.* submitted), and consequently lower ECM biomass, aggregate

stability should be lower. We worked in the field but at the species level in order to remove the confounding effect of mixed plant communities on our results.

2. Materials and methods

2.1. Field site and plant material

The work was conducted in the Massif du Grand Sud in New Caledonia at a site called Bois du Sud, located in a botanical reserve (22°10'S-166°46'E) (Fig. 1), at an altitude of 200-230 m. Mean annual precipitation is 3000 mm and the minimal and maximal mean annual temperatures are between 20.5 °C and 26.6 °C (Météo France 2016b). The site was selected according to three main criteria: (i) a Ferralsols on ultramafic substrates typical of the Massif du Grand Sud, (ii) a slope <30° subject to water erosion, and (iii) the three model species to be studied all present.

The three selected plant species were: *Costularia arundinacea* (Sol. Ex Vahl) Kük. (Cyperaceae), *Tristaniopsis glauca* Brongn. & Gris (Myrtaceae) and *Arillastrum gummiferum* (Pancher ex Brongn. & Gris) Baill. (Myrtaceae) (Fig. 2). All species are: associated with fungi; dominant species in shrubland and forest in the Massif du Grand Sud; and finally used for revegetation and ecological restoration purposes (L'Huillier *et al.* 2010). All three species are considered as having a positive impact on soil aggregate stability when present as dominant species in plant communities (Demenois *et al.* submitted-b). *C. arundinacea* is a perennial herbaceous plant which frequently dominates this stratum in sedge dominated communities. *C. arundinacea* is known to host plant growth promoting rhizobacteria (PGPR) and AMF (Lagrange *et al.* 2011). *T. glauca* is an ectomycorrhizal (ECM) host shrub (Amir and

148 Ducousso 2010) that grows in sclerophyllous shrubland and is ubiquitous and dominant in
149 shrublands of the Massif du Grand Sud. *A. gummiferum* is an ECM host tree (Papineau 1989)
150 which usually occurs in extensive, monodominant stands (Sebert 1874; Virot 1956) and
151 grows exclusively on ultramafic substrates.

152

153 ### *2.2. Field sampling*

154 For each species, twenty individuals were geo-tagged (Fig. 3). Plants were at least 1 m
155 distant from each other. As the age of the individuals was unknown, only specimens <2 m in
156 height were selected to standardize observations. Additionally, twenty wooden poles were
157 inserted into the soil and geo-tagged to mark control samples. Controls were characterized
158 by bare soil, without any plants present, and were within a radius of 0.5 m from the nearest
159 pole. For each plant individual (n = 60 plants), and control points (n = 20 points), four soil
160 samples were collected for root trait measurements, assessment of fungal biomass, soil
161 aggregate stability tests and soil analyses.

162

163 ### *2.3. Root trait measurements*

164 The method used to measure root traits of the three plant species was described in
165 Demenois *et al.* (submitted-c). Briefly, it consisted in collecting, for each plant and control
166 sample, soil samples (0 – 15 cm deep) at the base of each plant, using a cylindrical corer
167 (diameter 8 x length 15 cm) in order to obtain a soil volume of 754 cm^3. Roots were
168 extracted from the soil core by washing them with tap water in a column of two sieves (2.00
169 and 0.1 mm mesh size).

For root morphological measurements, one subsample of roots was selected and weighed (> 25 % of fresh weight). The root fragments were spread out to avoid root overlap in a layer of water and then scanned on a flatbed scanner (Epson Expression 10000XL) at a resolution of 600 dpi (Pierret *et al.* 2013). Specific root length (SRL), the percentages of very fine (VFR) (diameter < 0.2 mm) and fine (FR) (0.2 < diameter < 1 mm) roots, total root mass density (RMD) and root length density (RLD) were then measured.

2.4. Fungal biomass measurements

The method used to measure fungal biomass in the rhizosphere of the three plant species and the control was based on a quantitative PCR approach (qPCR) (Chemidlin Prévost-Bouré *et al.* 2011; Wallander *et al.* 2013). The approach is described in Demenois *et al.* (submitted-c) and briefly consisted in collecting 50 ml of soil in a Falcon tube at the base of each plant. These soil samples were conserved in an ice box in the field and then taken to the laboratory on the same day and stored at -20°C. Each soil sample was lyophilised for 48 h. Then 5 g of soil from each sample was homogenized in a mortar and pestle with liquid nitrogen, and DNA was extracted from 0.25 g subsample of each soil sample using the Mo Bio PowerSoil DNA extraction kit (Fierer *et al.* 2012). As purified soil DNA extracts may still contain PCR inhibitors, serial dilutions of the DNA templates (1/10 to 1/1000) were used to determine the amount of DNA to be used in the real-time qPCR assay. FR1 and FF390 primers (Vainio and Hantula 2000) were chosen as they are relevant for a robust and specific detection of the soil fungal community (Chemidlin Prévost-Bouré *et al.* 2011). The qPCR products obtained from the DNA of a pure culture of *Cortinarius sp.* (strain FC12-35-1 from IAC fungal collection) were cloned in a plasmid (pGEM-T Easy Vector System, Promega, France) and used as standard for the real-

time qPCR assay after quantification with a Nanodrop 2000 Spectrophotometer (ThermoScientific™, USA). Fungal biomass is expressed in number of copies of 18S rDNA gene per g of soil.

2.5. Soil aggregate stability tests

The method used to measure aggregate stability of the three plant species and the control consisted of collecting, for each individual and control sample (n = 3 replicates per treatment), soil samples (0 – 15 cm deep) at the base of each plant, using a cylindrical corer (diameter 8 x length 15 cm). Then, soil aggregate stability was measured according to the standardized method NF X 31–515 (Afnor 2005) derived from Le Bissonnais (1996) and Le Bissonnais and Arrouays (1997). We focused on the most disruptive test consisting of quick immersion in water, which induces a slaking action typical of heavy precipitation events (Demenois et al 2017b submitted). In compliance with the norm NF X 31-515, when the percentage of gravel was ≥ 40 %, MWD value was not validated and excluded in further analyses.

2.6. *Soil analyses: SOC and sesquioxides*

For each plant and control, one half liter of soil was collected at the base of each plant. For each sample, soil organic carbon (SOC), iron (Fe) and aluminium (Al) sesquioxides were measured using Walkley and Black (1934) and Mehra (1958) methods, respectively.

2.7. *Data analyses*

To investigate the relationships between root traits and plant species, a principal component analysis (PCA) was performed. Differences in root traits, fungal biomass, soil analyses and soil aggregate stability were assessed using Kruskal and Wallis tests, followed by Wilcoxon tests to specify pairwise differences.

To investigate the relationships between soil aggregate stability, root traits, fungal biomass and soil characteristics, a PCA was performed on the matrix of variations between each species and the control. Correlations were explored with a Spearman correlation test. All statistical analyses were performed using the R.3.3.2. environment for statistical computing (R Core Team 2016).

3. Results

3.1. Root characteristics

Each of the three species was characterized by specific root traits. The projection of plant species on axes 1 and 2 of the PCA clearly discriminated the three species (Fig. 4). The first and second principal components explained 46 % and 28 % of the total variance, respectively. Axis 1 was positively correlated with the percentage of very fine roots and RLD. In contrast, Axis 1 was negatively correlated with the percentage of fine roots.
A. gummiferum was characterized by a high percentage of very fine roots and RLD (Fig. 4). *C. arundinacea* and *T. glauca* were equally distributed along the first axis, with a high percentage of fine roots (Fig. 4). Axis 2 of the PCA was positively associated with RMD and negatively with SRL. Axis 2 discriminated *C. arundinacea* from *T. glauca* and *A. gummiferum* (Fig. 4), *C. arundinacea* being characterized by high RMD (Fig. 4).

237 The species-related root traits were confirmed by the Kruskal and Wallis tests and pairwise
238 Wilcoxon rank sum tests (Table 1). *A. gummiferum* possessed a significantly higher
239 percentage of very fine roots (49 ± 10 %), compared to *C. arundinacea* (23 ± 6 %) and
240 *T. glauca* (25 ± 7 %) (Table 1). In contrast, the latter two species had significantly higher
241 percentages of fine roots (*C. arundinacea*: 71 ± 5 %, *T. glauca:* 69 ± 8 %) compared to
242 *A. gummiferum* (48 ± 9 %) (Table 1).

243 RLD for *A. gummiferum* was also significantly higher (223 ± 215 $km.m^{-3}$) compared to
244 *T. glauca* (19 ± 23 $km.m^{-3}$, Table 1). However, no significant differences in RLD were found
245 between *A. gummiferum* and *C. arundinacea* (141 ± 90 $km.m^{-3}$, Table 1). The same trend was
246 observed for RMD, with *C. arundinacea* (12.8 ± 10.5 $kg.m^{-3}$) and *A. gummiferum* (9.9 ± 10.3
247 $kg.m^{-3}$), having significantly higher values than *T. glauca* (1.8 ± 2.5 $kg.m^{-3}$, Table 1). Finally,
248 *A. gummiferum* possessed a significantly higher SRL (25.9 ± 9.6 $m.g^{-1}$) compared to the
249 *C. arundinacea* (12.4 ± 3.4 $m.g^{-1}$) and *T. glauca* (15.9 ± 12.1 $m.g^{-1}$, Table 1).

250

251 ### *3.2. Fungal biomass*

252 Significant differences of fungal biomass were shown beneath each plant species despite a
253 high variability (Fig. 5). Soil beneath *C. arundinacea* contained a significantly higher mean
254 number of copies of 18S rDNA gene per g of soil compared to the two other species and the
255 control (Fig. 5). Similarly, the number of copies of 18S rDNA gene per g of soil under
256 *A. gummiferum* was significantly higher than for the control (Fig. 5).

257

258 ### *3.3. Soil aggregate stability*

259 Beneath each of the three species and the control, MWD was >2 mm which meant that soil
260 aggregates were very stable (Fig. 6). In soil under *C. arundinacea*, MWD was significantly
261 higher than for the control (Fig. 6) and variability of MWD was low compared to that for the
262 two other species and the control (Fig. 6). In contrast, no significant differences in MWD
263 were found between *T. glauca*, *A. gummiferum* and the control (Fig. 6).

264

265 3.4. *Soil SOC and sesquioxides*

266 SOC was significantly higher beneath all three species compared to the control (Table 3).
267 Significantly higher values were found beneath *C. arundinacea* (19.9 ± 5.2 $mg.g^{-1}$, Table 3)
268 and *A. gummiferum* (17.6 ± 5.4 $mg.g^{-1}$, Table 3) compared to *T. glauca* (11.9 ± 2.1 $mg.g^{-1}$,
269 Table 3).

270 Fe-sesquioxides were remarkably high (> 34 %) beneath all three species as well as the
271 control (Table 3). Significantly different values were measured between the three species
272 and the control with the highest values found beneath *T. glauca* (Table 3). The same trend
273 was observed for Al-sesquioxides. However, in comparison to Fe-sesquioxides, the content
274 of Al-sesquioxides was low (< 30 $g.kg^{-1}$, Table 3).

275

276 *3.5. Relationships between soil aggregate stability, root traits and mycorrhiza*

277 According to the results of the PCA (Fig. 7), positive correlations between the variations of
278 MWD, the percentage of fine roots, SOC and RMD were expected, while negative
279 correlations between the variations of MWD and Fe-sesquioxides occurred. The first and
280 second principal components explained respectively 29 % and 26 % of the total variance (Fig.

281 7). Axis 1 was positively correlated with RLD, RMD and SOC and negatively correlated with
282 Fe-sesquioxides (Fig. 7). Axis 2 was positively correlated with the percentage of very fine
283 roots and SRL and negatively correlated with the percentage of fine roots and MWD (Fig. 7).

284 Spearman's correlation tests confirmed the relationships between the observed variations of
285 MWD between the three species and controls and RMD, SOC and Fe-sesquioxides (Fig. 8).
286 Significant positive correlations were found for SOC and RMD, while a significant negative
287 correlation was observed for Fe-sesquioxides (Fig. 8). Besides, RLD was positively correlated
288 with SOC and negatively with Fe-sesquioxides, while Al-sesquioxides was positively
289 correlated with Fe-sesquioxides (Fig. 8).

290

291 **4. Discussion**

292 *4.1. Relationships between soil aggregate stability and plant species*

293 Surprisingly, soil aggregate stability beneath both *T. glauca* and *A. gummiferum* was similar
294 to that found in the controls (bare soil). These results are unexpected as in general, plant
295 roots increase soil structural stability (Li *et al.* 1992) through the enmeshment of particles,
296 drying of the soil environment around roots, supplying of decomposable organic residues
297 and substrates for microorganisms (Amézketa 1999). However, significantly higher values of
298 SOC and fungal biomass were found in the rhizosphere of *T. glauca* and *A. gummiferum*
299 (both ECM-hosts) compared to the controls. Increases in SOC also increase soil aggregate
300 stability (Erktan *et al.* 2016), and the positive influence of mycorrhizal fungi on aggregate
301 stability has been well documented (Degens 1997; Rillig and Mummey 2006). However, in
302 these Ferralsols, aggregate stability was always high, even in the control bare soils, with a

303 mean MWD >2 mm, as also found by Demenois *et al.* (submitted-b) working at the same
304 sites but at the plant community level. This high stability was likely due to the content of Fe-
305 and Al-sesquioxides (> 35 %) (Demenois *et al.* submitted-b; Le Bissonnais and Singer 1993).
306 Therefore, we suggest that on Ferralsols on ultramafic substrates and at the scale of isolated
307 ECM-hosts, the very high content of Fe- and Al-sesquioxides masks any influence of roots,
308 ECM and SOC on soil aggregate stability.

309 In contrast, we found that soil aggregate stability beneath *C. arundinacea* had improved
310 compared to bare soil. This result is consistent with the idea that monocotyledons are
311 superior to dicotyledons for the stabilizing of aggregates because the former contain a much
312 larger root biomass with more exudates present (Amézketa 1999; Glinski and Lipiec 1990).
313 Unlike *T. glauca* and *A. gummiferum, C. arundinacea* is an AMF-host (Lagrange *et al.* 2011),
314 and several studies across diverse soil types have demonstrated that AMF hyphae and
315 associated chemical complexes such as the glycoprotein, glomalin (Wright and Upadhyaya
316 1998), are significant contributors to aggregate stability (Rillig *et al.* 2002). The qPCR
317 approach used in our study targeted only DNA from fungal mycelium, therefore the
318 influence of glomalin and fungal exudates was not quantified, and they may have more
319 influence on soil aggregate stability than the physical enmeshing of soil by fungal mycelium.
320

321 The ability of *C. arundinacea* to increase soil aggregate stability compared to *T. glauca* and *A.*
322 *gummiferum* might also reveal different behaviors concerning C mineralization, as
323 significantly different SOC values were found in soils from beneath each species. According
324 to Martins and Angers (2015), plant species can be classed into two contrasting groups, with
325 differential positive effects on SOC and soil water stable macroaggregates. Type-*K* plants

would be characterized by a low mineralization rate of the labile C pool and a high mineralization rate of the non-labile C pool, while type-*B* plants have the opposite pattern. Type-*K* plants would be characterized by long-lasting water stable macroaggregates more useful at preventing soil erosion, whereas type-*B* plants would be adequate for soil management strategies aimed at C sequestration (Martins and Angers 2015). Therefore, according to our results, *C. arundinacea* would be a type-*K* species, typical for pioneer grasses and herbaceous species, while *T. glauca* and *A. gummiferum* would be type-*B* species, as usually found for shrubs and trees. *C. arundinacea* is also a sedge that does not shed its leaves; leaves remain attached to the base of the stem and slowly decompose, therefore soil C from decomposing leaf litter will stay close to the plant, in the area that we sampled. *T. glauca* and *A. gummiferum* both shed their leaves slowly throughout the year, and the strong winds to which these sites are exposed can cause leaf litter to be blown away from the parent plant, especially in shrubland dominated by *T. glauca*, which possesses smaller leaves.

4.2. Relationships between soil aggregate stability, root traits, mycorrhiza and soil characteristics

All species had a low SRL with a maximum value of 25.9 ± 9.6 $m.g^{-1}$ for *A. gummiferum*. Such low values may be because Ferralsols on ultramafic substrates are very deficient in P, K and Ca (L'Huillier *et al.* 2010). The higher SRL and percentage of very fine roots of *A. gummiferum* are typical of species that are less dependent on mycorrhizal associations than in more coarse root systems (Brundrett 1991). This result may explain the lower fungal biomass measured in the rhizosphere of *A. gummiferum* compared to *C. arundinacea*. On Ferralsols

on ultramafic substrates, P uptake is one of the main constraints for plant growth (L'Huillier *et al.* 2010). P is deficient and retained by the iron oxides resulting in a very low assimilable fraction (<30 $mg.kg^{-1}$) (L'Huillier *et al.* 2010). Plants can increase the availability of P through different strategies such as dauciform roots (Lambers *et al.* 2006; Miller 2005; Shane *et al.* 2005), already observed in *C. arundinacea* (Lagrange *et al.* 2011). Dauciform roots form during short periods of a plant's life and exude organic acids to facilitate nutrient uptake from soils (Lambers *et al.* 2008). Microbial activity can be inhibited by dauciform roots, but our results did not suggest that fungal biomass was reduced beneath *C. arundinacea*.

We found a significant and positive correlation between SOC and MWD, as also found by e.g. Erktan *et al.* (2016); Le Bissonnais and Arrouays (1997). SOC increases the stability of soil aggregates through several direct and indirect mechanisms (Abiven *et al.* 2009): SOC (i) binds mineral particles which increases soil aggregate stability (Chenu 1989; Tisdall and Oades 1982), and (ii) protects soil against slaking and reduces aggregate wettability (Chenu *et al.* 2000; Le Bissonnais and Arrouays 1997), favoring the formation of stable aggregates. Additionally, for herbs such as *C. arundinacea*, SOC likely comprises easily decomposable components (Freschet *et al.* 2013; Garnier *et al.* 2004), known to stimulate microorganisms exuding hydrophilic polysaccharides, hence increasing inter-particle cohesion.

For all species, a significant and positive correlation was found between RMD and MWD, and an indirect positive correlation with RLD. High RMD or RLD should increase soil aggregate stability (Miller and Jastrow 1990; Pérès *et al.* 2013), but as MWD beneath *A. gummiferum* was not significantly different to that in bare soil, an increase of RMD or RLD alone might not be sufficient for increasing aggregate stability in these conditions. *C. arundinacea* is a cespitous plant with an adventitious root system (L'Huillier et al. 2010) and so possessed

372 higher RMD, RLD as well as percentage of fine roots compared to the two other species
373 (both are taprooted species), suggesting that it is the combined effects of these root traits
374 that increased soil aggregate stability beneath this species.

375 We found a significant and negative correlation between MWD and Fe sesquioxides which
376 was unexpected as Fe sesquioxides usually have a positive stabilizing effect on micro-
377 aggregates (Amézketa 1999). It has been suggested that Fe sesquioxides act as a cement
378 between mineral and organic particles (Barthès *et al.* 2008; Le Bissonnais and Singer 1993).
379 However, at our study site, the content of Fe sesquioxides was extremely high, with values
380 above 300 g kg^{-1}, while the values found by Le Bissonnais and Singer (1993) and Barthès et
381 *al.* (2008) did not exceeded 100 g kg^{-1}. Therefore, we hypothesize that at a given level of Fe
382 sesquioxides, micro-aggregate stability values reached a plateau and Fe sesquioxides had no
383 further influence on stability. Beyond this point, stability would be influenced by other
384 factors such as SOC content. Thus, the negative correlation found between MWD and Fe
385 sesquioxides was the consequence of the negative correlations between Fe sesquioxides and
386 SOC and does not reveal a causal link between MWD and Fe sesquioxides.

387

388 *4.3. Relationships between soil aggregate stability, plant richness and diversity*

389 We found that soil aggregate stability measured at the species scale beneath *C. arundinacea*
390 was comparable to that measured at the community scale in *T. glauca* shrubland, *Arillastrum*
391 or mixed rainforests (Demenois *et al.* submitted-b). This finding is contradictory to results
392 from recent studies which highlighted the influence of plant richness and diversity on soil
393 aggregate stability in annual or perennial grasslands (Erktan *et al.* 2016; Jastrow 1987; Pohl

et al. 2009). It has been hypothesized that plant diversity promotes the formation and stabilization of soil aggregates *via* several mechanisms. For example, plant communities with contrasting tissue chemical characteristics, which affect the decomposability of their organic matter, are likely to enhance aggregate stability at different time scales (Abiven *et al.* 2009). Similarly, soil microbial biomass (Eisenhauer *et al.* 2010; Pérès *et al.* 2013) and SOC (Erktan *et al.* 2016; Steinbeiss *et al.* 2008) should increase with plant diversity due to species complementarity, quality of rhizodeposits and higher root biomass production. We found that SOC and fungal biomass were positively correlated to soil aggregate stability at both the species and community scales (Demenois *et al.* submitted-c). Therefore, our results highlight the efficiency of *C. arundinacea* as a useful ecological engineering species (Ghestem *et al.* 2014) for increasing soil aggregate stability, and hence it's potential for the revegetation or restoration of degraded Ferralsols on ultramafic substrates.

In contrast, MWD beneath isolated *T. glauca* and *A. gummiferum* was lower than that measured at the community scale in *T. glauca* shrubland and *Arillastrum* rainforest (Demenois *et al.* submitted-b). These results are consistent with those found by Erktan *et al.* (2016), who showed that species richness and diversity were positively related to soil aggregate stability. Therefore, further investigations should be carried out at different scales to determine if plant and microbial species grown in association have a greater effect on aggregate stability than when grown in isolation in the same communities. As suggested by Erktan *et al.* (2016), we also found that higher MWD in diverse *T. glauca* shrubland and *Arillastrum* rainforest (in comparison to isolated *T. glauca* and *A. gummiferum),* was likely related to the accumulation of SOC. Plant communities with high species richness and diversity generally produce more aboveground biomass than less diverse plant communities

(Hooper *et al.* 2005), and aboveground biomass is positively correlated to MWD because of the input of C from leaf litter (Demenois *et al.* submitted-c). Leaf litter with contrasting properties from different plant species is be a good substrate for a more diverse range of soil meso- and microorganisms (Eisenhauer *et al.* 2011; Wardle *et al.* 2004). The discrepancy in results between different scales illustrates the difficulty to define rules for ecological restoration and emphasizes the need to identify efficient communities for improving soil quality and conservation.

5. Conclusion

We showed that on Ferralsols on ultramafic substrates, different plant root traits and associated mycorrhizas produced diverse impacts on soil aggregate stability. MWD was highest in soil beneath *C. arundinacea* (an AMF-host in the Cyperaceae family), characterized by high RMD, RLD, percentage of fine roots and high fungal biomass, compared to that beneath individuals of the shrub *T. glauca* and the tree *A. gummiferum*. MWD in the rhizosphere of these latter two species was also similar to that of bare soil. Fe- and Al-sesquioxides were very high in all soil samples, therefore, we suggest that at the scale of isolated ECM-hosts, any influence of roots, ECM and SOC on aggregate stability was masked by the intrinsic nature of the Ferralsol. Nevertheless, further investigations should be carried out to explore more thoroughly the influence of plant roots and soil micro-organisms on aggregate stability at both the individual and community level, in order to devise efficient strategies for the ecological restoration of degraded soils.

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674 produced by hyphae of arbuscular mycorrhizal fungi. *Plant and Soil* **198**, 97-107.

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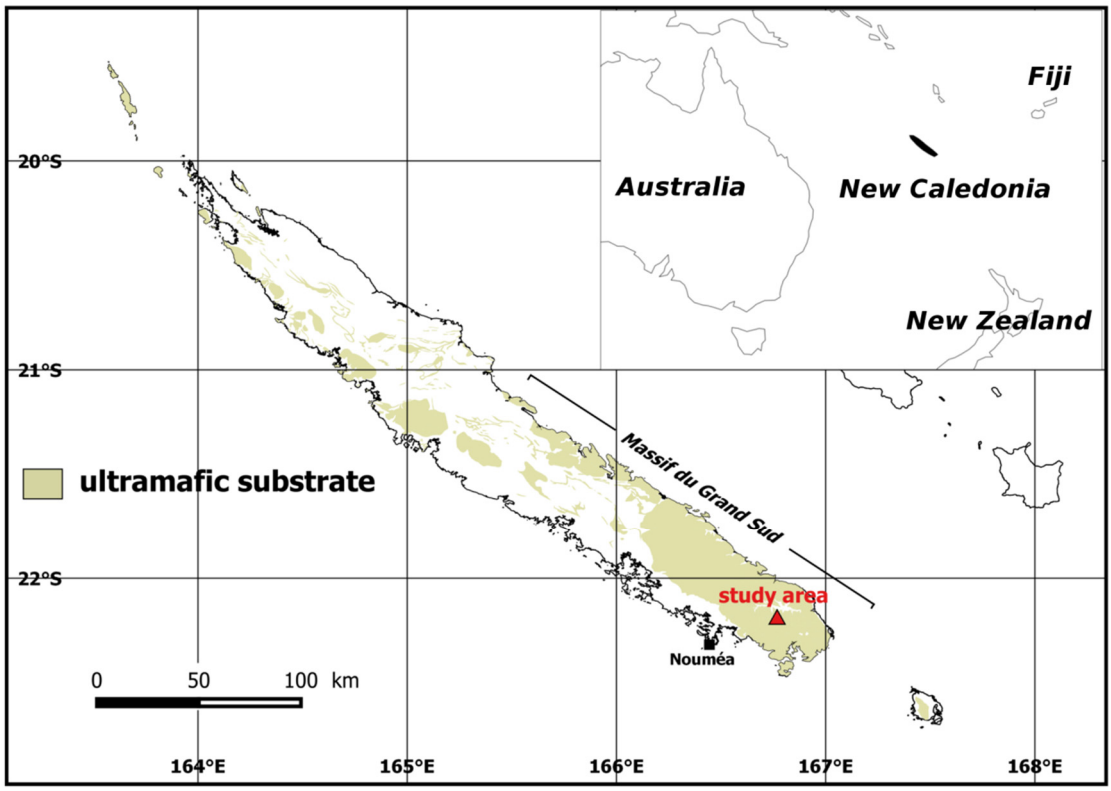
677

678 **Figure captions**



679

680 **Fig. 1. Location of New Caledonia in the south west Pacific and distribution of ultramafic substrates**
681 **in the archipelago.** The study area is located in the Massif du Grand Sud and is indicated by the
682 triangle.

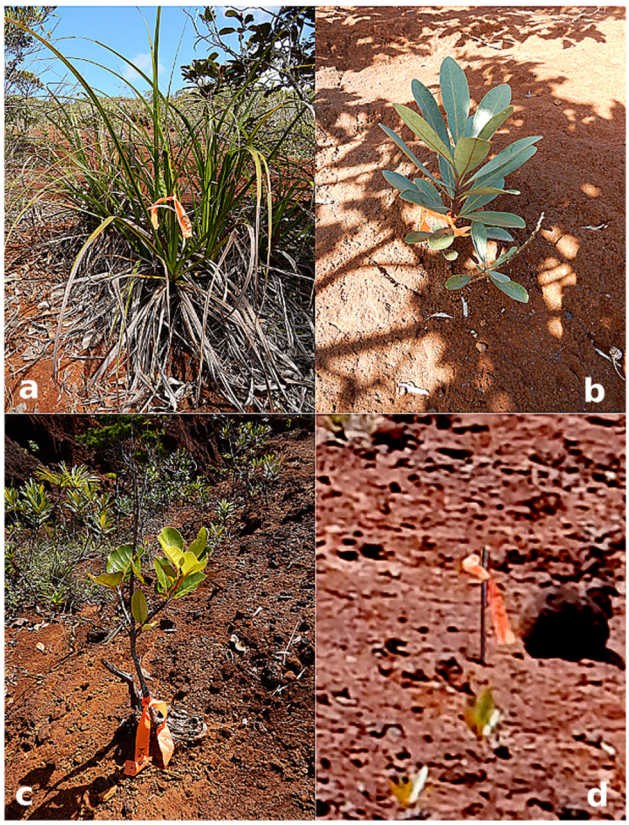
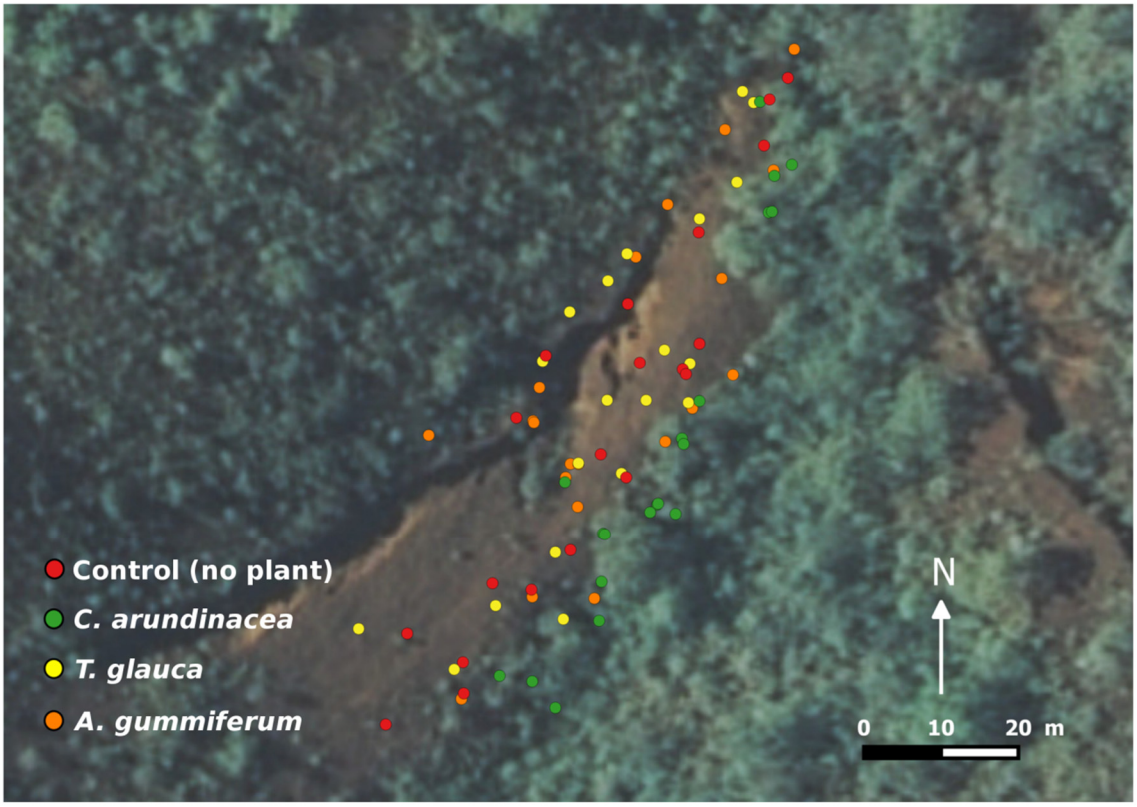


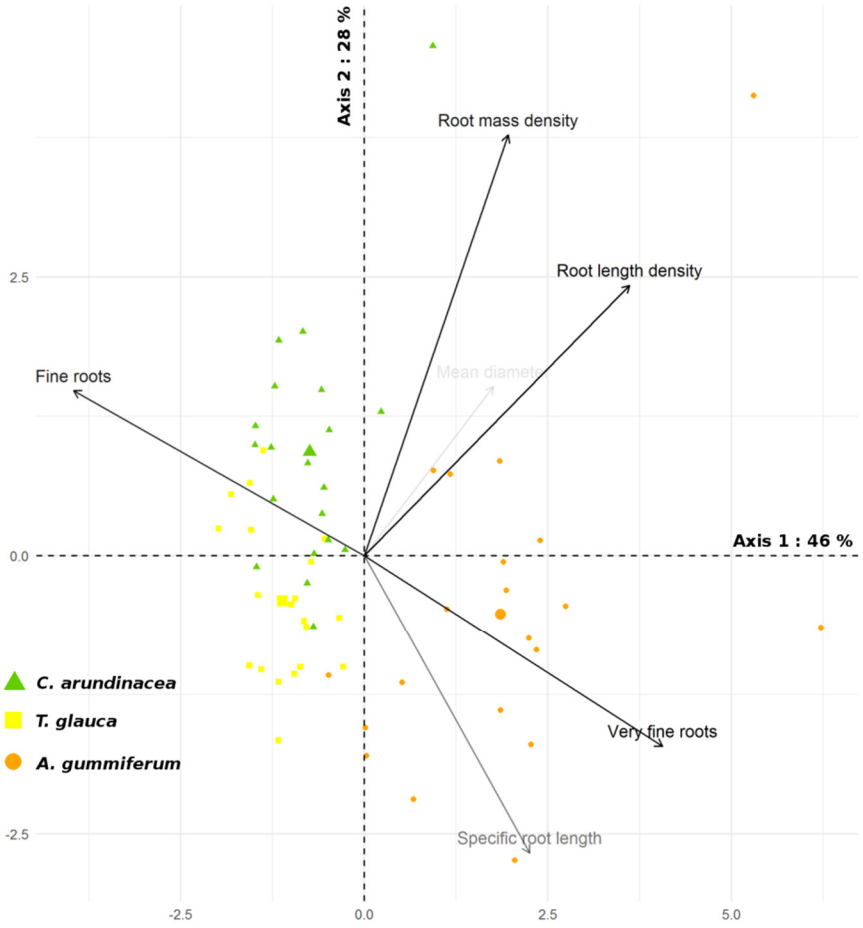
Fig. 2. Plant species studied and control sample. a: *Costularia arundinacea* (arbuscular mycorrhiza); b: *Tristaniopsis glauca* (ectomycorrhiza); c: *Arillastrum gummiferum* (ectomycorrhiza); d*:* control (no plant).



688

689 **Fig. 3. Location of the sampling points at the study site.**

690



691

692 **Fig. 4. Principal component analysis of plant root traits for the three plant species.** Larger symbols
693 indicate the center of cluster of traits of each species. Cos^2 for variables are shown using the color
694 scale: light grey <0.4; grey 0.4< < 0.8; black >0.8.

695

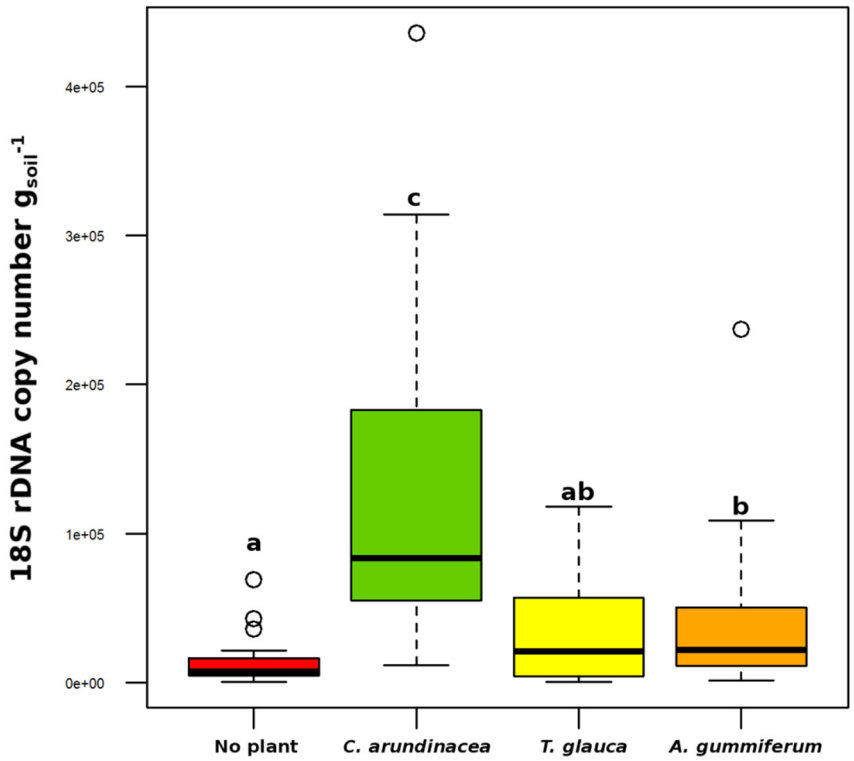
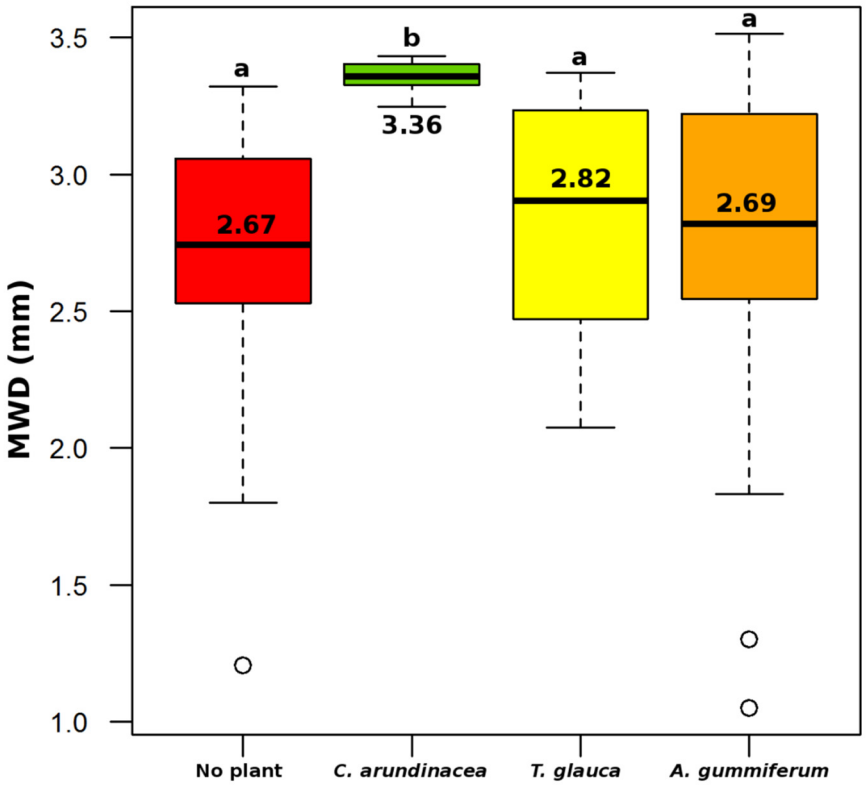


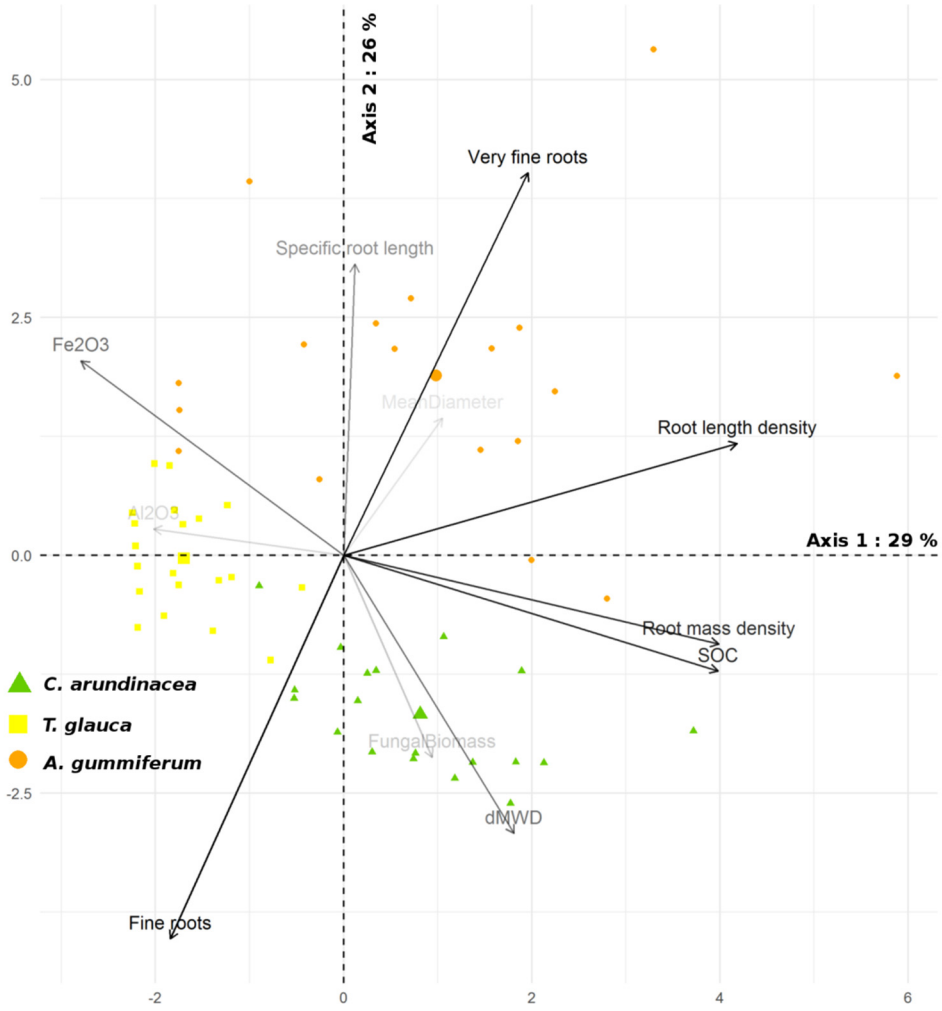
Fig. 5. Variations of 18S rDNA gene copy number in soil beneath each plant species and in control soil. Mean values are given for each species and control. Letters indicate significant differences between species or control given by a pairwise Wilcoxon rank sum test (P<0.05).



701

702 **Fig. 6. Soil aggregate stability (MWD) beneath the three plant species and in the control sample.**
703 Mean values are given for each species and control. Letters indicate significant differences between
704 species or control given by a pairwise Wilcoxon rank sum test (see Table 2).

705



706

707 **Fig. 7. Principal component analysis for differences in soil aggregate stability (dMWD) between the**
708 **three plant species the control.** Larger symbols indicate the center of cluster of traits of each
709 species. Cos^2 for variables are shown using the color scale: light grey <0.4; grey 0.4< < 0.8; black >0.8.

710

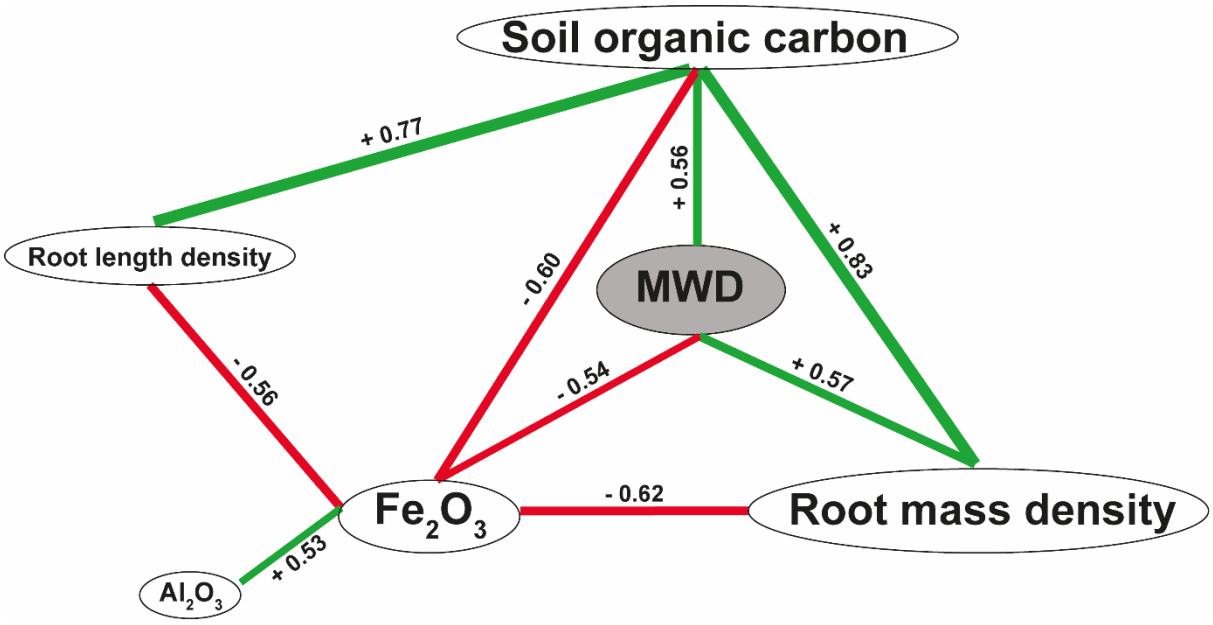


Fig. 8. Spearman's correlations for differences in soil aggregate stability between the control, three plant species and the variables from the principle component analysis shown in Fig.7. Only correlations with ρ> 0.5 with *P*<0.001 are shown. Indicated values are for *ρ*. Green color for the lines indicates a positive correlation while red lines are negatively correlated.

Tables

Table 1. Statistical tests on root traits for the three plant species. Data are average value ± standard error for each plant species (n=20) and significant differences between plant species are indicated by Kruskal-Wallis test (X^2/*P*). Letters indicate significant differences between plant species given by pairwise Wilcoxon rank sum test. Levels of significance are n.s.: non-significant; ***: *P*<0.001.

Variable (Abb./unit)	*Costularia arundinacea*	*Tristaniopsis glauca*	*Arillastrum gummiferum*	Kruskal-Wallis test (X^2/*P*)
Root length density (RLD / km.m^{-3})	141 ± 90 a	19 ± 23 b	223 ± 215 a	28.88/***
Root mass density (RMD / kg.m^{-3})	12.8 ± 10.5 a	1.8 ± 2.5 b	9.9 ± 10.3 a	25.17/***
Specific root length (SRL / m.g^{-1})	12.4 ± 3.4 a	15.9 ± 12.1 a	25.9 ± 9.6 b	20.62/***
Mean root diameter (mm)	0.44 ± 0.05 a	0.43 ± 0.10 a	0.50 ± 0.23 a	0.81/n.s.
Fine roots (0.2< <1 mm) (%)	71 ± 5 a	69 ± 8 a	48 ± 9 b	36.88/***
Very fine roots (<0.2 mm) (%)	23 ± 6 a	25 ± 7 a	49 ± 10 b	37.17/***

Table 2. Statistical tests on soil aggregate stability beneath the three plant species and the control. Kruskal-Wallis and pairwise Wilcoxon rank sum test of soil aggregate stability of the three species and control (no plant). Bold numbers indicate significant p-values (*P*<0.001).

Aggregate stability ~ plant species	X^2 = 36.444, ***p*-value = 6.033 x 10^{-8}**, df = 3		
	No plant	***Costularia arundinacea***	***Tristaniopsis glauca***
Costularia arundinacea	**2.3 x 10^{-5}**	-	-
Tristaniopsis glauca	0.69	**2.7 x 10^{-4}**	-
Arillastrum gummiferum	0.94	**4.3 x 10^{-4}**	0.94

Table 3. Statistical tests on soil organic carbon, iron sesquioxides and aluminium sesquioxides for soil from beneath the three plant species and control soil. Data are means ± standard error for each species / control (n=20) and significant differences are indicated by Kruskal-Wallis tests (X^2/*P*). Letters indicate significant differences between species / control given by pairwise Wilcoxon rank sum tests. Levels of significance are ***: *P*<0.001.

Variable (Abb./unit)	Control (no plant)	*Costularia arundinacea*	*Tristaniopsis glauca*	*Arillastrum gummiferum*	Kruskal-Wallis test (X^2/*P*)
Soil organic carbon (SOC / $mg.g^{-1}$	7.5 ± 1.8 a	19.9 ± 5.2 b	11.9 ± 2.1 c	17.6 ± 5.4 b	56.15/***
Fe-sesquioxides (Fe_2O_3 / $g.kg^{-1}$)	336 ± 19 a	365 ± 29 b	428 ± 13 c	395 ± 37 d	51.74/***
Al-sesquioxides (Al_2O_3 / $g.kg^{-1}$)	15 ± 8.5 a	18.5 ± 9.1 ab	23.6 ± 2 c	18.2 ± 8.5 b	27.65/***

Does arbuscular and ectomycorrhizal fungal inoculation improve soil aggregate stability? A case study on three tropical species growing in ultramafic Ferralsols

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Abstract

In many tropical regions, such as New Caledonia, soil erosion from anthropogenic activities and subsequent ecological restoration are major issues. Revegetation could be an efficient way to mitigate this risk. Some plant species are more useful for stabilizing soil aggregates and thus reducing erodibility. Similarly, associated mycorrhizas influenced aggregate stability. Here, we examined if plant inoculation with arbuscular (AMF) and ectomycorrhizal (ECM) fungi could improve the soil aggregate stability of ultramafic Ferralsols. To this purpose, we carried out inoculations with local AMF and ECM on three endemic plant species of New Caledonia grown in greenhouse: the sedge *Costularia arundinacea* (Sol. Ex Vahl) Kük*.,* an AMF (arbuscular mycorrhizal fungi) host, the shrub *Tristaniopsis glauca* Brongn. & Gris and the tree *Arillastrum gummiferum* (Pancher ex Brongn. & Gris) Baill*.,* both of the latter are ectomycorrhizal fungi (ECM) hosts. The experiment consisted of three treatments for each plant species. The treatments were as follows: untreated ultramafic topsoil (control), plants only and plants inoculated. Inoculation of *C. arundinacea* was carried out by adding a suspension of spores*. T. glauca* and *A. gummiferum* were inoculated with *Pisolithus microcarpus*. For each planted treatment, 20 plants were harvested 9 months after AMF inoculation and 10 months after ECM inoculation. Above- and below-ground dry biomass, root traits, soil organic carbon and soil aggregate stability were measured and compared to the control.

We showed that, on ultramafic topsoil, AMF and ECM inoculation could significantly increase the plant growth, modify the root traits and consequently enhance the soil aggregate stability, root length density appearing to be the most contributive factor. Among the three species, the root traits of *C. arundinacea* were the most efficient to stabilize soil aggregates.

Additionally, we identified a functional and efficient plant – fungus association (*T. glauca* – *Pisolithus microcarpus*) to facilitate the plant growth and stabilize soil.

These findings are of particular interest for revegetation, erosion control or ecological restoration of ultramafic substrates in New Caledonia. They confirm that the application of indigenous plant species with carefully selected mycorrhizal fungi could be an efficient eco-engineering measure to initiate and accelerate the recolonisation of bare slopes.

Highlights

- Soil aggregate stability on ultramafic topsoil was significantly increased by AMF and ECM inoculation
- Root length density was the most contributive factor to soil aggregate stability
- *Costularia arundinacea* was the most efficient tested plant to stabilize soil aggregates
- *'Tristaniospsis glauca + Pisolithus microcarpus'* was identified as a functional and efficient plant – fungus association to facilitate the plant growth and stabilize soil aggregates

Keywords

Mycorrhizal symbiosis, root traits, ecological restoration, ultramafic substrates, New Caledonia

3. Introduction

Soil aggregate stability influences a wide range of physical and biogeochemical processes in the natural environment (Amézketa 1999). For instance, stable soil aggregates are more resistant to detachment and loss through erosion (Barthès and Roose 2002; Pierson and Mulla 1990). Fungi contribute to soil aggregation and stabilization at different spatial scales directly by charge, adhesive, and enmeshment mechanisms (Rillig and Mummey 2006; Tisdall and Oades 1982). Their influence has been demonstrated several times for arbuscular mycorrhizal fungi (AMF) (Bedini *et al.* 2009; Martin *et al.* 2012; Miller and Jastrow 2000; Rillig *et al.* 2002; Ritz and Young 2004; Tisdall and Oades 1982), but remains unclear for ectomycorrhizal fungi (ECM) (Demenois *et al.* submitted-c; Graf and Frei 2013).

In a previous study carried out *in situ* on ultramafic Ferralsols, Demenois *et al.* (submitted-b) assessed the influence of fungal biomass on soil aggregate stability and suggested that AMF contributed more than ECM to its increase. Yet, as mycorrhizas modify the root architecture and their root traits (Garbaye 2013), it was neither possible to untangle the direct nor the indirect effect of mycorrhizas through their host plants (Graf and Frei 2013).

Assessing the influence of mycorrhizas on aggregate stability of ultramafic Ferralsols is of particular interest for ecological restoration. Indeed, in ultramafic ecosystems, most of the plants are known to be involved in mycorrhizal associations to face the extreme soil conditions (Alexander *et al.* 2007; Branco 2010; Schechter and Bruns 2008). AMF and ECM associations are known to significantly enhance plant nutrition such as P assimilation, and to strongly reduce abiotic stresses on plants such as metal toxicity (Jourand *et al.* 2014; Smith and Read 2010). Besides, in New Caledonia, a hotspot of biodiversity (Myers *et al.* 2000), ultramafic substrates are prone to intense erosion (Dugain 1953). As a consequence, erosion

control and ecological restoration are major issues, especially on heavily eroded sites (Losfeld *et al.* 2015).

Thus, in this study, we explored how AMF and ECM inoculations could improve the soil aggregate stability of ultramafic Ferralsols. The main hypothesis was that the inoculation with AMF or ECM should increase the soil aggregate stability directly through enmeshment by fungal hyphae and by the production of organic components, and indirectly by accelerating the plant growth and modifying the root traits. To test this hypothesis and identify the main factors, we carried out inoculations with AMF and ECM on three plant species of New Caledonia grown in greenhouse on ultramafic topsoil.

4. Materials and methods

4.1. Selected plant species and soil material

Three plant species were selected: *Costularia arundinacea* (Sol. Ex Vahl) Kük. (Cyperaceae), *Tristaniopsis glauca* Brongn. & Gris (Myrtaceae) and *Arillastrum gummiferum* (Pancher ex Brongn. & Gris) Baill. (Myrtaceae). All of them are dominant species of Ferralsols in New Caledonia and are known to influence the soil microbial richness, composition and abundance (Gourmelon *et al.* 2016). The three species are used for revegetation, erosion control and ecological restoration in New Caledonia (L'Huillier *et al.* 2010) and are suspected to have a potential positive impact on the soil aggregate stability when frequent in plant communities (Demenois *et al.* 2017).

Costularia arundinacea (Fig. 1a) is a perennial herbaceous that frequently dominates this stratum in sedge dominated communities. *C. arundinacea* is known to host arbuscular

mycorrhiza (AMF) (Lagrange *et al.* 2011). *Tristaniopsis glauca* (Fig. 1b) is a shrub growing in open sclerophyllous shrubland. The species is ubiquitous and dominant in shrublands. It is associated with ectomycorrhizal fungi (ECM) (Amir and Ducousso 2010). *Arillastrum gummiferum* (Fig. 1c) is a tree which usually occurs in extensive, monodominant stands (Sebert 1874; Virot 1956). It grows exclusively on ultramafic substrates and is associated with ECM (Papineau 1989).

For the purpose of this experiment, *Costularia arundinacea* (Cyperaceae) seed lot n°05/07/15, *Tristaniopsis glauca* (Myrtaceae) seed lot "Col des Dalmates, 29/05/2015" and *Arillastrum gummiferum* (Myrtaceae) seed lot n°005/14 were collected respectively in La Tontouta, les Dalmates and Bois du Sud, New Caledonia by IAC. Seeds were washed three times for five minutes in sterile water, then surface sterilized for five minutes in NaClO (1.25%) and finally washed three times for five minutes in sterile water. The seeds of *C. arundinacea* and *T. glauca* were pre-germinated in trays containing sterile perlite, while seeds of *A. gummiferum* were pre-germinated in sterile Petri dish. After 31, 86 and 7 days respectively, seedlings were transplanted into sterile plastic containers of 1 liter capacity and filed with ultramafic topsoil that had been previously screened on a 5 mm mesh and autoclaved two times in 48 h at 120°C for 60 min. This soil (sandy loam) was collected at 0 - 10 cm depth from Rivière des Pirogues (22°12'S-166°44'E), New Caledonia, and is typical of Ferralsol on ultramafic substrates. It contained 58 % of sand, 24 % of silt, 18 % of clay, < 0.5 % of soil organic carbon and > 25 % of iron sesquioxides.

4.2. Fungal inocula

The ectomycorrhizal inoculum applied was originally isolated from fruit bodies of *Pisolithus microcarpus* (strain PISO 4, IAC herbarium) collected under *Arillastrum gummiferum* trees. The identification of the fungus, *Pisolithus microcarpus,* was performed by sequencing the rDNA internal transcribed spacer (ITS), a region used for DNA barcode in fungi (Schoch *et al.* 2012). The ITS was amplified using the fungus-specific primer ITS1f (Gardes and Bruns 1993) and the Basidiomycetes-specific primer LB-W (Tedersoo *et al.* 2008). Sequencing was realised using ITS1 (White *et al.* 1990) or ITS1f primers and the reverse ITS4 primer (White *et al.* 1990) at the 'Plate-Forme du Vivant de la Nouvelle-Calédonie' (PFV-NC) (Nouméa, New Caledonia) using the Big Dye Sequencing Kit v.3.1 (Applied Biosystems, Foster City, CA, USA). The generated sequence was edited with Sequencher v.4.10.1 (Gene Codes Inc., Ann Arbor, MI, USA). Taxonomic assignment was carried out by comparing ITS sequence to UNITE and INSD databases.

Pisolithus microcarpus isolate was obtained by aseptically transferring a piece of the body fruit to solid Melin-Norkrans Medium (MNM) (Marx 1969). Inoculum was prepared as described in Brundrett *et al.* (1996) by incubating fungal mycelium from cultures on Petri dishes inoculated into 2 l of sterile solid substrate (peat-perlite mixture, 1:10, v:v), saturated with MNM liquid media in large plastic bags (5 l). The incubation was carried out at 30°C in a dark room for eight weeks. Seven month-old *T. glauca* and *A. gummiferum* were inoculated with 10 ml of 8-week-old mycelial inoculum. To mimic the potential physiological stress induced by the inoculation, 10 ml of sterile peat-perlite mixture was applied on non mycorrhized plants.

Arbuscular mycorrhiza inoculation of *C. arundinacea* was carried out three months after transplantation by adding 10 ml of a suspension of spores (approx. 100 spores ml^{-1})

146 extracted from soil collected in monodominant *Arillastrum gummiferum* rainforest in the
147 rhizosphere of *C. arundinacea,* following Brundrett *et al.* (1996) protocol to separate AMF
148 fungus spore from soil.
149
150 *4.3. Plant growth and treatments*

151 The experiment consisted of three treatments for each plant species. The treatments were
152 as follows: (1) untreated sterilized soil sample (control); (2) *C. arundinacea*, *T. glauca* or
153 *A. gummiferum* plants without being inoculated (further indicated as non mycorrhized); and
154 (3) *C. arundinacea*, *T. glauca* or *A. gummiferum* inoculated plants (mycorrhized).
155 Plants were grown in the greenhouse under a natural light cycle during 9 months after
156 inoculation for the herbaceous species and 10 months for the two woody plants. Water was
157 applied by spraying 2 min, 6 times per day. The watering system operated day and night. No
158 fertilization was applied after inoculation. All experiments were carried out on six
159 independent assays (non mycorrhized *vs* mycorrhized for the three species), with each
160 planted treatment containing at least 50 plant replicates. Controls (30 in total) were equally
161 distributed among the planted treatments. For all treatments, plants were moved randomly
162 every four weeks to avoid neighboring and border effects.
163
164 *4.4. Analyses*

165 Nine months after AMF inoculation, 20 plants of *C. arundinacea* were randomly selected and
166 harvested. Ten months after ECM inoculation, for both *T. glauca* and *A. gummiferum*,
167 20 plants were randomly selected and harvested. Additionally, all the controls (10 per plant

168 species) were collected. Directly after harvesting, the plant shoots were collected, fresh
169 weighted then lyophilized during 24 h to obtain the above-ground dry biomass (AGB).
170 Directly after harvesting, water stability of aggregates for the three treatments was also
171 measured according to the protocol of Burri *et al.* (2009). A sieve with mesh openings of
172 20 mm was placed in a bucket (3 l). The sieve and the bucket were both placed in a larger
173 bucket (10 l). After the greenhouse period, each sample was put singly on the sieve.
174 Subsequently, the two buckets were filled with water entirely covering the sample. After
175 5 min, the water was drained. In a next step, the roots of planted as well as of planted and
176 inoculated samples were carefully removed. Then, the soil portion remaining on the sieve
177 and the one passing were separately oven dried for 24 h at 105°C. The soil aggregate
178 stability was defined as the dry weight ratio between the components above the sieve and
179 the sum of all components, above and below the sieve.
180 The roots were cleaned, fresh weighted, spread out in a water-filled transparent plastic
181 container. For root morphological measurements, one subsample of roots (~ 25 % of fresh
182 weight) was selected and weighted. The roots were spread out in a thin layer of water in a
183 glass container (40 x 30 x 2 cm), in order to avoid root overlap, and scanned on a flatbed
184 scanner (Epson Expression 10000XL) at a resolution of 600 dpi (Pierret *et al.* 2013). Analyzed
185 roots were subsequently recovered and oven dried at 60 °C during 72 h, and weighted to
186 obtain their dry mass (Pérez-Harguindeguy *et al.* 2013). Root images were analyzed with the
187 open source solution IJ_Rhizo (Pierret 2013, http://www.plant-image-analysis.org). Total
188 root length (Kimura length) and the length of roots in 254 diameter classes (0.085 mm width
189 from 0 to above 21.5 mm) were measured by the software. Specific root length (SRL) was
190 calculated as the ratio between total root length and root dry mass. The percentages of very

191 fine (diameter < 0.2 mm) and fine (0.2 - 1 mm diameter) roots were defined as the ratio of
192 length in the concerned root classes to the total root length (Miller and Jastrow 1990). Total
193 root mass density (RMD) corresponds to the ratio between the total root dry mass and the
194 soil volume from which roots were extracted (1 l). The root length density (RLD) was
195 calculated as RLD = SRL x RMD. Total root dry mass (BGB) was calculated from the total root
196 fresh weight and the humidity percentage of the roots obtained from the dry subsamples.
197 Root mass fraction was defined as the ratio between the total root dry mass and the total
198 dry mass of the plant.
199 To assess the efficiency of the plant species to increase soil aggregate stability, two ratios
200 were calculated. The first one consisted in the ratio between the variations of soil aggregate
201 stability in comparison to their respective control divided by the total root dry mass
202 (δAS/BGB). The second ratio was defined as the ratio between the variations of soil
203 aggregate stability in comparison to their respective control divided by the Kimura root
204 length of the plant (δAS/root length). The rationale of these two ratios was to assess the
205 influence of a given mass or length of root on soil aggregate stability, which seems relevant
206 for the purpose of ecological restoration in very infertile soils like ultramafic topsoil.
207 The AMF mycorrhization of *C. arundinacea* was verified for each plant. To this purpose, roots
208 were stained with Trypan blue (Koske and Gemma 1989). For each individual sample, at least
209 10 root segments of 1 cm length were mounted in 10 % glycerol on glass slides for
210 examination with a light microscope. A root segment was considered to be mycorrhized
211 when arbuscules, vesicules or hyphal coils were clearly identified.
212 Similarly, for *T. glauca* and *A. gummiferum*, the ECM mycorrhization was checked on a root
213 subsample under a stereo microscope. Observed ectomycorrhizae were collected for each

mycorrhized plant and placed in an Eppendorf tube containing CTAB 2x buffer (100 mM Tris HCl (pH 8), 1.4 M NaCl, 20 mM Na2 EDTA, 2% CTAB). The identification of the fungus was performed as previously indicated by sequencing the ITS region.

Mycorrhizal dependency was calculated by expressing the difference between the total dry weight of the mycorrhizal and non-mycorrhizal plants as a percentage of the total dry weight of the mycorrhizal plants (Plenchette *et al.* 1983). Finally, for each treatment, soil organic carbon (SOC) was measured following Walkley and Black (1934) method. Soil analyses were carried out at IRD Nouméa by the US191 IMAGO LAMA.

4.5. Statistics

Differences in soil aggregate stability between treatments and plants were assessed using Kruskal and Wallis tests, followed by one-sided Wilcoxon-Mann-Whitney rank sum tests to specify pairwise differences, as higher soil aggregate stability was hypothesized for mycorrhized plants. Differences in root traits and SOC between treatments and plants were assessed using pairwise Wilcoxon-Mann-Whitney rank sum tests. Correlations between soil aggregate stability and variables (root traits and SOC) were explored with Spearman correlation test. All statistical analyses were performed using the R 3.3.2 environment for statistical computing (R Core Team 2016).

5. **Results**

5.1. Fungal inoculum

AMF and ECM mycorrhization were checked on all the harvested plants. Seventeen plants of *C. arundinacea* were confirmed to be mycorrhized, while 11 plants were confirmed as non mycorrhized (Fig. 2a). For *T. glauca*, 11 plants were confirmed as mycorrhized, while 20 plants were confirmed as non mycorrhized (Fig. 2b). Finally, for *A. gummiferum*, 15 plants were confirmed as mycorrhized, while 19 plants were confirmed as non mycorrhized (Fig. 2c). Seven and 8 ectomycorrhizae were successfully sequenced from *T. glauca* and *A. gummiferum*, respectively. Molecular taxonomic assignments confirmed that the observed ectomycorrhizae belonged to *Pisolithus microcarpus* (99 % similarity).

5.2. Plant growth

AMF mycorrhization of *C. arundinacea* induced enhancement of plant growth when compared with non mycorrhized plants (Table 1). Below-ground dry biomass and total dry biomass of *C. arundinacea* significantly increased (Table 1). Similarly, ECM mycorrhization of *T. glauca* with *P. microcarpus* enhanced above- and below-ground plant growth (Table 1). In contrast, ECM mycorrhization of *A. gummiferum* with the same strain did not enhance plant growth (Table 1). Besides, for the three plant species, root mass fraction was not modified by the inoculation (Table 1). Finally, *C. arundinacea* and *T. glauca* showed a higher mycorrhizal dependency than *A. gummiferum* (Table 1).

5.3. Root traits

AMF mycorrhization of *C. arundinacea* induced a significant increase of RLD (Table 1). In contrast, the other root traits were not modified by the AMF mycorrhization (Table 2).

For *T. glauca*, ECM mycorrhization induced significant increases of all root traits except for the percentage of very fine roots and the mean diameter (Table 2). In contrast, ECM mycorrhization of *A. gummiferum* with the same strain did not modify significantly the root traits measured (Table 2).

5.4. SOC

AMF mycorrhization of *C. arundinacea* did not induce any significant modification of SOC (Table 2), contrary to ECM mycorrhization of *T. glauca* and *A. gummiferum.*

5.5. Soil aggregate stability

AMF mycorrhization of *C. arundinacea* increased significantly soil aggregate stability compared to the non mycorrhized plants (Fig. 3). Additionally, *C. arundinacea* increased significantly the aggregate stability compared to the control (Fig. 3).

Similarly, ECM mycorrhization of *T. glauca* with *Pisolithus microcarpus* increased significantly the aggregate stability compared to the non mycorrhized plants and to the control (Fig. 3). Additionally, *T. glauca* increased significantly the aggregate stability compared to the control (Fig. 3).

In contrast, for *A. gummiferum,* the influence of ECM mycorrhization with *Pisolithus microcarpus* on aggregate stability was not significant, as well as the plant alone (non mycorrhized treatment) (Fig. 3). However, for $P < 0.1$, a significant difference of aggregate stability was found between the control and the mycorrhized treatments (Fig. 3).

Finally, comparisons of the efficiency of the plant species to increase soil aggregate stability (δAS / BGB and δAS / root length) revealed a significantly higher efficiency of *C. arundinacea*

compared to the two other species (Table 3). Interestingly, the efficiency was significantly enhanced by ECM mycorrhization of *T. glauca* with *Pisolithus microcarpus* (Table 3). No such effect of the mycorrhization was observed for *C. arundinacea* and *A. gummiferum*.

6. Discussion

6.1. Influence of AMF and ECM inoculations on plant growth

Our results showed that AMF and ECM inoculations increased the plant growth of *C. arundinacea* and *T. glauca* (Table 1) on ultramafic topsoil, while no significant effect on plant growth was found for *A. gummiferum*. This result for *C. arundinacea* was consistent with a previous study on endemic Cyperaceae of New Caledonia (Lagrange *et al.* 2011). Mycorrhizal inoculation with AMF is known to improve plant growth by leading to an increase of total P and N accumulated in each plant (Smith and Read 2010), and by contributing to plant K uptake, and improve host plant heavy metal tolerance (Marschner 2012). Additionally, Lagrange *et al.* (2011) showed that even a low level of root colonization with AMF would be sufficient to increase the plant absorption and consequently the plant growth, because of the low concentrations of mineral elements needed by the plants of the genus *Costularia* (Lagrange 2009).

Similarly, the promotion of plant growth by ECM symbiosis has been widely reviewed (Brundrett *et al.* 1996; Jourand *et al.* 2014; Smith and Read 2010). ECM associations are known to affect plant root growth, improve the general plant mineral nutrition and so improve plant fitness (Marschner 2012). Therefore, the influence of ECM *Pisolithus microcarpus* on plant growth of *T. glauca* was consistent with those previous studies.

Besides, *T. glauca* showed a higher mycorrhizal dependency than *A. gummiferum,* as already

303 suggested by Demenois *et al.* (submitted-a). Thus, those findings are of particular interest to
304 accelerate the revegetation of degraded ultramafic topsoil, as a functional plant – fungus
305 association (*T. glauca* with *Pisolithus microcarpus*) was clearly identified. In contrast, the
306 absence of significant effect on plant growth of controlled inoculation of *A. gummiferum*
307 with the same strain was unexpected. Yet, Jourand *et al.* (2014) showed that the impact of
308 controlled ECM inoculation on plant growth is plant and strain specific. Indeed, the
309 specificity and efficiency of ECM symbiosis is, for instance, at least influenced by the capacity
310 of plants to allocate carbon to ECM (Nehls and Hampp 2000). Besides, *Pisolithus microcarpus*
311 might not be involved in the plant growth of *A. gummiferum,* but could play a role in its
312 protection against pathogens or its survival, as the functions of ECM are known to be very
313 diverse (Smith and Read 2010).
314
315 *6.2. Influence of AMF and ECM inoculations on root traits*

316 We showed in this study that AMF and ECM inoculations modified some root traits of
317 *C. arundinacea* and *T. glauca* on ultramafic topsoil, while no significant changes of root traits
318 were found for *A. gummiferum*. For AMF inoculation, its effect on plant growth and
319 therefore RLD may range from positive to neutral or even negative (Klironomos 2003), as
320 this type of symbiosis can be seen as a continuum from parasitism to mutualism (Johnson *et*
321 *al.* 1997). In our study, the combination of *C. arundinacea* with local spores of AMF induced
322 a positive response on plant growth and consequently on RLD (Table 2), which emphasizes
323 the potential interest of such an association to boost the revegetation of degraded
324 ultramafic topsoil. Yet, characterization of the AMF community and identification of the
325 strains would be necessary to clearly identify the appropriate combinations plant-fungus.

For *T. glauca*, most of the root traits (e.g. RLD, RMD, SRL and the percentage of fine roots) were increased by the ECM *Pisolithus microcarpus*. This result is consistent with a study on *Alnus incana* and *Melanogaster variegatus s.l.* (Graf and Frei 2013), in which RLD of 5 month-old plants almost triple because of ECM inoculation. In contrast, the significant increase of SRL consequently to ECM inoculation was in discrepancy with results on *Fraxinus uhdei* associated with *Pisolithus tinctorius* (Ambriz *et al.* 2010). SRL and fine roots have been linked to rapid resource acquisition (Comas *et al.* 2002), suggested to form part of a single root trait spectrum representing the trade-off between nutrient conservation and acquisition (Larson and Funk 2016; Roumet *et al.* 2006). High SRL may allow rapid uptake of water, and enhance exploitation of soil nutrients and water (Eissenstat 1991) and is commonly, but not always, associated with rapid growth, its effect possibly being context-dependent (Larson and Funk 2016). Thus, ECM *Pisolithus microcarpus*, by modifying SRL and the percentage of fine roots of *T. glauca,* enhances nutrient acquisition and plant growth.

6.3. AMF and ECM inoculations improve soil aggregate stability

Through this study, we demonstrated that AMF and ECM inoculations improved soil aggregate stability even if the range of the positive influence varied between the three plant species. For *C. arundinacea*, our finding was expected. Indeed, according to Leifheit *et al.* (2014), a clear overall positive effect of AMF on soil aggregate stability was widely demonstrated for several plant species, fungus and soil types. However, to our knowledge, this if the first time that it is shown on ultramafic topsoil. Fungi are considered temporary binding agents by Tisdall and Oades (1982). AMF participate to aggregate stability through various mechanisms (e.g. glomalin) at different spatial scales (Graf and Frei 2013; Wright and

Upadhyaya 1998). The mycorrhizal fungi also affect indirectly the soil aggregate stability through their host plants, particularly by accelerating the development of their root network and by serving as a distribution vector for associated micro-organisms (Graf and Frei 2013). For *T. glauca* and *A. gummiferum*, the positive influence of ECM inoculation on aggregate stability was consistent with previous works (Ambriz *et al.* 2010; Graf and Frei 2013). Yet, similar to AMF inoculation, such a stabilizing effect of ECM inoculation was never shown on ultramafic topsoil. The filamentous growth-form of *Pisolithus microcarpus* and the mycelial networks far beyond the rhizosphere make it perfectly adapted in view of soil aggregation and stabilization. Indeed, in the manner of roots but on a smaller scale, hyphae enmesh and entangle small inorganic and organic soil particles (Miller and Jastrow 2000; Tisdall and Oades 1982). Besides, the production of polysaccharides and hydrophobines strongly supports a functional role in soil aggregate formation (Caesar-Ton That *et al.* 2001; Mankel *et al.* 2002; Tagu *et al.* 2001). These direct stabilizing effects of *Pisolithus microcarpus* could explain the higher aggregate stability for mycorrhized *A. gummiferum,* as root traits were unchanged by the inoculation. In contrast, for *T. glauca*, it is not possible to fractionate the contribution of roots and fungi. Indeed, ECM inoculation was responsible for significant changes in root traits (e.g. RLD), and for a higher SOC content which is commonly associated to an increase of aggregate stability (Graf and Frei 2013; Six *et al.* 2004; Tisdall and Oades 1982).

Conclusion

We showed that, on ultramafic topsoil, AMF and ECM inoculations could significantly increase the plant growth, modify the root traits and consequently enhance the soil

aggregate stability. Among the three species, the root traits of *C. arundinacea* were the most efficient to stabilize soil. Additionally, we identified a functional and efficient plant – fungus association, *T. glauca – P.microcarpus*, to facilitate the plant growth and stabilize soil. These findings are of particular interest for erosion control and ecological restoration of ultramafic substrates in New Caledonia and confirm that the application of indigenous plant species with carefully selected mycorrhizal fungi could be an efficient eco-engineering measure to initiate and accelerate the recolonisation of bare slopes.

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Figure captions

Fig. 1. Studied species in greenhouse conditions. a: 12 month-old mycorrhized *Costularia arundinacea* ; b: 17 month-old mycorrhized *Tristaniopsis glauca*; c: 17 month-old mycorrhized *Arillastrum gummiferum.*

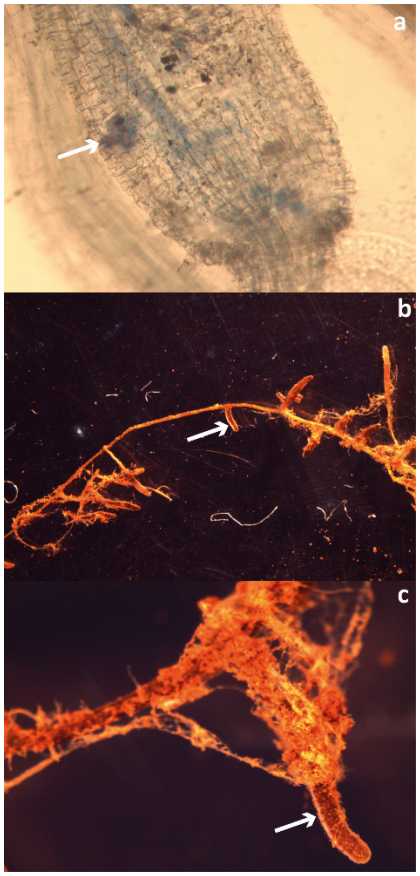
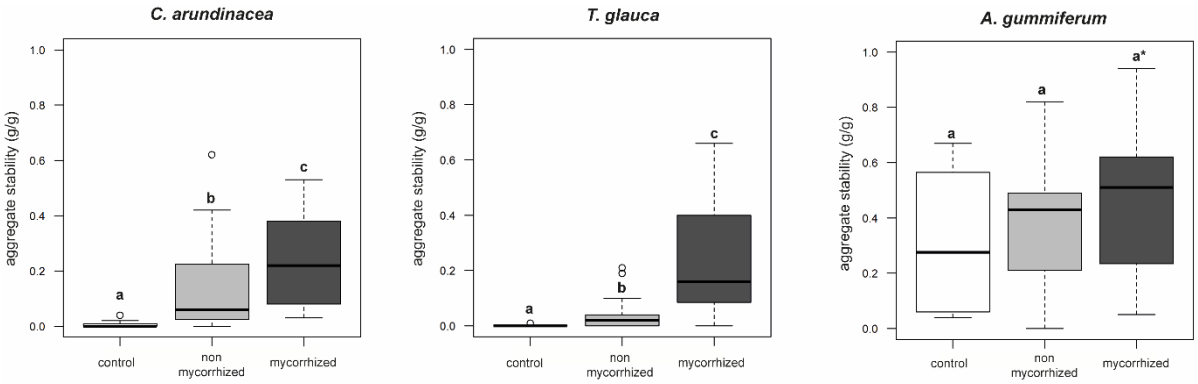


Fig. 2. Mycorrhized roots of the three species observed under stereo microscope. a: AMF stained with Trypan blue on a root of *Costularia arundinacea* (100 x magnification); b: ECM root tips on *Tristaniopsis glauca* (7.3 x magnification); c: ECM root tips on *Arillastrum gummiferum* (32 x magnification). White arrows show AMF and ECM root tip.



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592 **Fig. 3. Soil aggregate stability under the three species for the three treatments.** Different letters
593 indicate significant ($P < 0.05$) differences between treatments given by one-sided Mann-Whitney-
594 Wilcoxon rank sum test. * indicates a significant difference at $P < 0.1$ between the control and the
595 mycorrhized treatments.

Tables

Table 1. Effect of mycorrhization on plant growth of the three plant species studied

Variables (Abb./unit)	*Costularia arundinacea*		*Tristaniopsis glauca*		*Arillastrum gummiferum*	
	non mycorrhized *(n=11)*	***mycorrhized (AMF)*** *(n=17)*	***non mycorrhized*** *(n=20)*	***mycorrhized (ECM)*** *(n=11)*	***non mycorrhized*** *(n=19)*	***mycorrhized (ECM)*** *(n=15)*
Above-ground dry biomass (AGB) (g)	0.09 ± 0.06	0.12 ± 0.05	***0.18 ± 0.09***	***0.28 ± 0.15***	0.67 ± 0.23	0.73 ± 0.20
Below-ground dry biomass (BGB) (g)	***0.10 ± 0.07***	***0.16 ± 0.08***	***0.18 ± 0.07***	***0.30 ± 0.18***	0.75 ± 0.31	0.71 ± 0.29
Total dry biomass (TDB) (g)	***0.19 ± 0.14***	***0.27 ± 0.13***	***0.36 ± 0.14***	***0.58 ± 0.31***	1.42 ± 0.48	1.44 ± 0.47
Root mass fraction (RMF)	0.54 ± 0.05	0.57 ± 0.07	0.52 ± 0.11	0.53 ± 0.09	0.52 ± 0.07	0.48 ± 0.06
Mycorrhizal dependency	30%		38%		1%	

Data are average value ± standard error for each plant species. *n* indicates the number of plant for each treatment.
Bold italic indicates significant differences (P<0.05) between treatments given by one-sided Mann-Whitney-Wilcoxon rank sum test.

Table 2. Effect of mycorrhization on root traits and SOC for the three plant species studied

Variables (Abb./unit)	*Costularia arundinacea*		*Tristaniopsis glauca*		*Arillastrum gummiferum*	
	non mycorrhized *(n=11)*	***mycorrhized (AMF)*** *(n=17)*	***non mycorrhized*** *(n=20)*	***mycorrhized (ECM)*** *(n=11)*	***non mycorrhized*** *(n=19)*	***mycorrhized (ECM)*** *(n=15)*
Root traits						
Root length density (RLD) ($km.m^{-3}$)	***7.9 ± 4.1***	***13.9 ± 7.0***	***9.1 ± 4.2***	***18.8 ± 10.4***	17.7 ± 11.1	24.0 ± 21.8
Root mass density (RMD) ($kg.m^{-3}$)	0.10 ± 0.07	0.15 ± 0.08	***0.19 ± 0.07***	***0.34 ± 0.21***	0.72 ± 0.36	0.71 ± 0.38
Specific root length (SRL) ($m.g^{-1}$)	90.4 ± 23.3	95.0 ± 17.5	***49.4 ± 14.7***	***60.2 ± 17.6***	23.3 ± 5.5	30.9 ± 12.5
Fine roots (0.2< <1 mm) (%)	63 ± 3	64 ± 6	***64 ± 7***	***69 ± 7***	72 ± 11	73 ± 9
Very fine roots (<0.2 mm) (%)	36 ± 5	35 ± 6	33 ± 8	28 ± 7	14 ± 8	16 ± 8
Mean root diameter (mm)	0.22 ± 0.02	0.23 ± 0.02	0.24 ± 0.03	0.25 ± 0.02	0.34 ± 0.04	0.33 ± 0.04
Soil						
Soil organic carbon (SOC) ($mg.g^{-1}$)	7.05 ± 1.26	5.97 ± 2.04	***6.85 ± 1.69***	***8.33 ± 0.87***	***7.04 ± 0.80***	***8.07 ± 1.10***

Data are average value ± standard error for each plant species. *n* indicates the number of plant for each treatment.
Bold italic indicates significant differences ($P < 0.05$) between treatments given by pairwise Mann-Whitney-Wilcoxon rank sum test.

Table 3. Effect of mycorrhization on the efficiency of the plant species studied to increase soil aggregate stability

Variables (Abb./unit)	*Costularia arundinacea* [a]		*Tristaniopsis glauca* [b]		*Arillastrum gummiferum* [b]	
	non mycorrhized *(n=11)*	***mycorrhized (AMF)*** *(n=17)*	***non mycorrhized*** *(n=20)*	***mycorrhized (ECM)*** *(n=11)*	***non mycorrhized*** *(n=19)*	***mycorrhized (ECM)*** *(n=15)*
δAggregate Stability / BGB (δAS/BGB / g^{-1})	1.59 ± 2.19	1.44 ± 0.58	***0.24 ± 0.37***	***0.96 ± 0.96***	0.07 ± 0.32	0.22 ± 0.38
δAggregate Stability / Root length (δAS/root length / km^{-1})	20.89 ± 27.33	15.46 ± 5.54	***6.04 ± 10.55***	***16.15 ± 14.75***	2.77 ± 15.84	7.72 ± 16.25

Data are average value ± standard error for each plant species. *n* indicates the number of plant for each treatment.
Bold italic indicates significant differences ($P < 0.05$) between treatments given by pairwise Mann-Whitney-Wilcoxon rank sum test.
Different letters above the plant species indicate significant differences ($P < 0.05$) between species given by Mann-Whitney-Wilcoxon rank sum test.

Chapitre 5 – Discussion générale et perspectives

1. Un modèle d'organisation hiérarchique des agrégats influencé par les traits racinaires et les symbioses mycorhiziennes et dominé par les sesquioxydes de fer

Ce travail a permis de mettre en évidence l'influence des traits racinaires et des symbioses mycorhiziennes sur la stabilité des agrégats des Ferralsols sur substrats ultramafiques, que ce soit à l'échelle des communautés végétales (Chapitre 3) ou à l'échelle des espèces végétales (Chapitre 4). Ainsi, le rôle central de la longueur de racine par unité de volume (Root Length Density) et des racines fines sur la stabilité des agrégats a pu être identifié à ces deux échelles, tout comme celui des communautés fongiques (Chapitres 3 et 4) et des symbioses mycorhiziennes (Chapitre 4). A notre connaissance, ces résultats sont les premiers acquis sur Ferralsols développés sur substrats ultramafiques.

Ces résultats sont conformes au modèle d'organisation hiérarchique des agrégats du sol proposé par Tisdall and Oades (1982) (Fig. 17), montrant, s'il en était besoin, toute la pertinence de celui-ci (Jarvis *et al.* 2012). Pour mémoire, ce modèle décrit différents types de matières organiques en fonction de leur effet stabilisant et de leur échelle :

- des agents transitoires (*e.g.* polysaccharides) qui peuvent être décomposés rapidement par les micro-organismes du sol ;
- des agents temporaires (*e.g.* racines, filaments fongiques) ;
- des agents persistants (*e.g.* composés humiques associés à des cations métalliques : Fe^{3+}, Al^{3+}).

Ainsi, en dépit des spécificités des Ferralsols sur substrats ultramafiques (*i.e.* faible présence d'argiles minéralogiques de type 1 :1 ; présence d'argiles granulométriques due aux fortes teneurs en oxydes de fer ; teneurs élevées en nickel, chrome et cobalt), l'organisation hiérarchique de leurs agrégats ne diffère pas de celle rencontrée dans d'autres types de sol. En revanche, leur stabilité élevée (> 2 mm), y compris sur sol dénudé et érodé, est remarquable et nos résultats corroborent ceux de Oades and Waters (1991) sur Ferralsols. Cette forte stabilité des agrégats, malgré la quasi absence de matières organiques stabilisantes (*e.g.* maquis ligno-herbacés dégradés), s'explique très probablement par les fortes teneurs en sesquioxydes de fer et d'aluminium (> 35 %) que l'on rencontre dans les Ferralsols sur substrats ultramafiques.

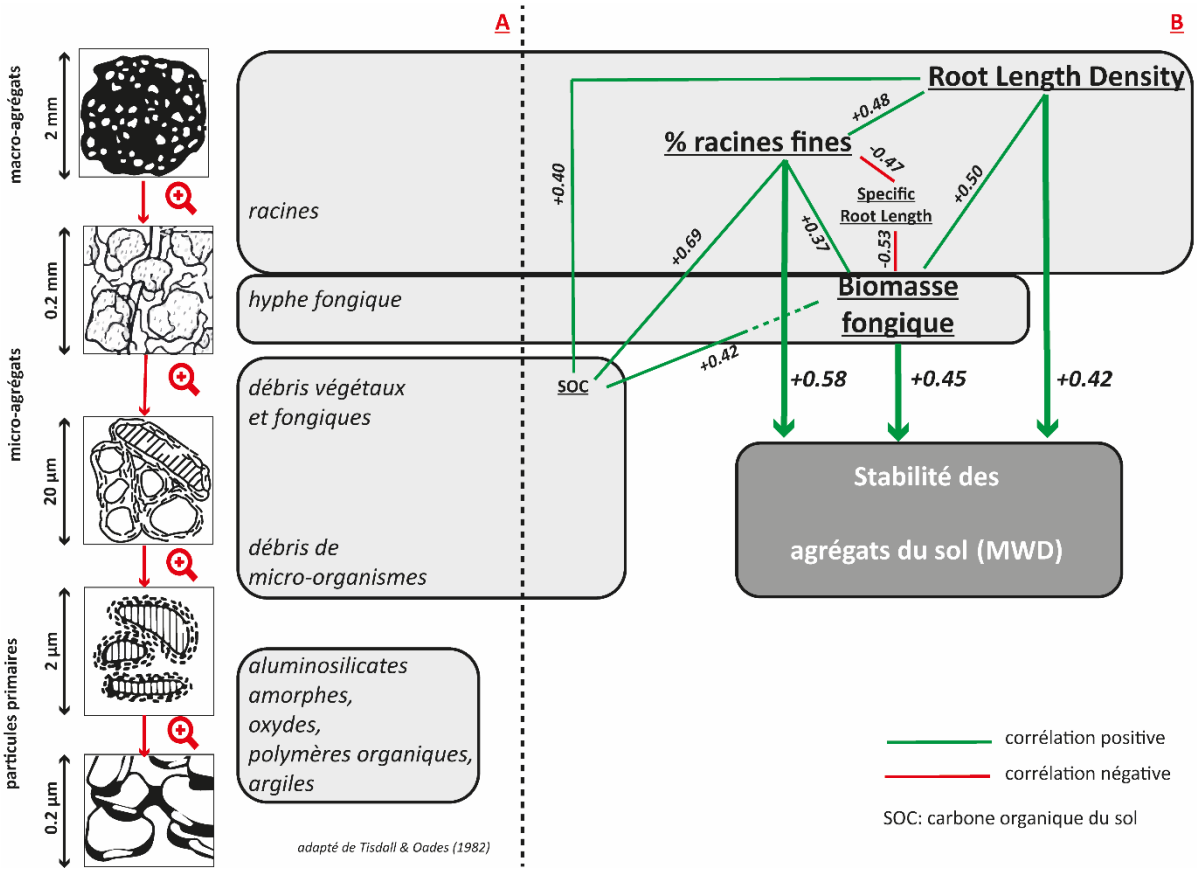

Figure 17 – A. Modèle d'organisation hiérarchique de Tisdall and Oades (1982) B. Corrélations de Spearman entre la stabilité des agrégats du sol, les traits racinaires et la biomasse fongique à l'échelle des communautés

Seules les corrélations avec $P<0.001$ sont représentées. Les valeurs indiquées sont celles de ρ. Les traits verts indiquent une corrélation positive et les trais rouges une corrélation négative. Les flèches indiquent les liens directs avec la stabilité des agrégats du sol (MWD).

En revanche, d'un point de vue méthodologique, la structure fréquemment gravillonnaire des Ferralsols à nodules ferrugineux (grenaille), liée aux mécanismes de dissolution-recristallisation sur substrats ultramafiques, peut rendre inapplicable l'utilisation de la norme Afnor (2005) NF X 31-515 permettant d'évaluer la stabilité des agrégats du sol. En effet, si le taux de gravier atteint 40 %, les résultats des tests ne sont alors plus valides. Or, il n'est pas rare de rencontrer sur le terrain des zones où la structure gravillonnaire est prépondérante (Fig. 18).

Figure 18 – Sol gravillonnaire sous *Arillastrum gummiferum* avec présence de mycélium (photos : J. Demenois sur la mine Montagnat à Tomo)

A : vue d'ensemble avec « tâche » de mycélium entourée en rouge ; B : zoom sur la « tâche » de mycélium

Aussi, afin d'évaluer la sensibilité à l'érosion de ces zones, est-il nécessaire d'envisager une approche méthodologique différente de celle de la norme Afnor (2005) NF X 31-515. Bast *et al.* (2015) proposent une méthodologie permettant d'évaluer un coefficient de stabilité des agrégats (*Aggregate Stability Coefficient* – ASC) sur des sols gravillonnaires. La méthode de prélèvement du sol sur le terrain est similaire à celle que nous avons utilisée. La carotte de sol est placée sur un tamis de maille 20 mm puis immergée pendant 5 min (Fig. 19). Les auteurs mettent en évidence une corrélation forte entre le MWD évalué selon une méthode proche de la norme Afnor (2005) NF X 31-515 et l'ASC sur Leptosol en climat sub-océanique. Il serait donc intéressant de tester cette approche méthodologique, proche de celle utilisée pour les essais en serre, afin d'évaluer la sensibilité à l'érosion dans davantage de configurations pédologiques, et notamment dans les lits de ravines.

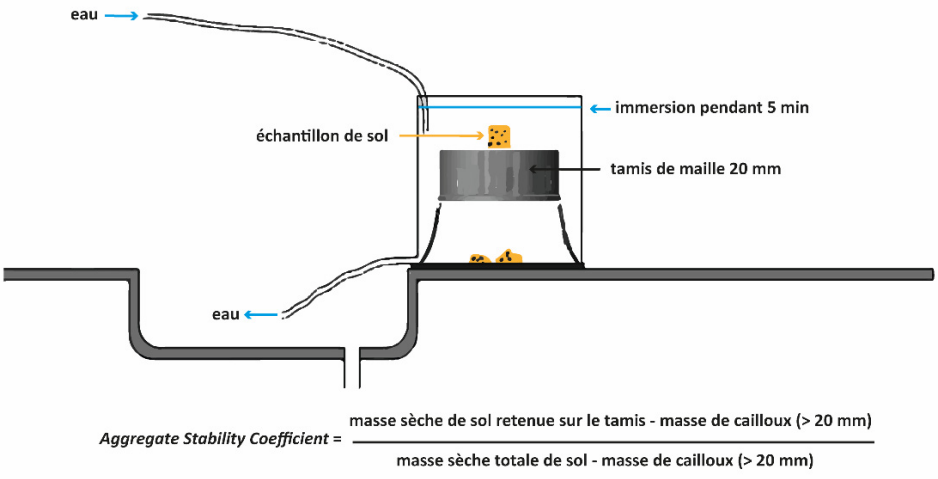

Figure 19 – Méthode d'évaluation de *l'Aggregate Stability Coefficient* (d'après Bast et *al.* 2015)

2. Le taux de couverture végétale et la compaction du sol comme seuils biotique et abiotique entre maquis ligno-herbacé et maquis ligno-herbacé dégradé

Si la forte stabilité des agrégats des Ferralsols sur substrats ultramafiques à l'échelle des communautés végétales (Chapitre 3) et des espèces végétales (Chapitre 4) atteste de leur faible sensibilité à l'érosion hydrique superficielle, l'aléa érosion à l'échelle d'un bassin versant va également dépendre de la pente, de la courbure des surfaces, du drainage et de sa densité, enfin de l'occupation du sol (Maurizot and Delfau 1995). En effet, l'érosion du sol combine à la fois la dégradation de sa couche superficielle mais aussi le déplacement des matériaux qui résultent de cette dégradation. Ainsi, des agrégats stables peuvent être déplacés du fait du ruissellement de l'eau et donc contribuer à l'érosion à l'échelle du bassin versant. Il est donc essentiel de prendre en compte le bilan hydrique (évapotranspiration, ruissellement, infiltration) à l'échelle du bassin versant pour évaluer l'aléa érosion.

En milieu tropical, ce bilan est largement influencé par la végétation : le retour d'eau vers l'atmosphère sous forme d'évaporation et de transpiration par la végétation y représente environ 80 % du bilan hydrique (Velluet *et al.* 2014). Il est donc fort probable qu'à pluviosité et stabilité des agrégats équivalentes, l'infiltration et le ruissellement de l'eau soient différents suivant le type de couverture végétale (*e.g.* maquis ligno-herbacé dégradé *versus* forêt monodominante à *Nothofagus aequilateralis*) et aient de fait un impact différent à l'échelle du bassin versant sur l'aléa érosion. De tels bilans hydriques sur Ferralsols sur substrats ultramafiques n'ont à ce jour pas été établis en Nouvelle-Calédonie et permettraient de mieux comprendre l'influence des formations végétales sur l'érosion hydrique à l'échelle du bassin versant.

De plus, l'érosion hydrique superficielle peut évoluer vers une érosion hydrique concentrée à l'origine de l'arrachement de volumes plus importants de sol et aboutissant à des formes d'érosion allant des griffes d'érosion (< 2 cm de profondeur) jusqu'à de grandes ravines (> 2 m de profondeur) (Rouet 2009). Ce dernier type de forme d'érosion est très fréquent en Nouvelle-Calédonie sur Ferralsols sur substrats ultramafiques (Fig. 20). Enfin, l'érosion à l'échelle du bassin versant pourra être également provoquée par les phénomènes de chutes de blocs rocheux et de mouvements de masse, et ce d'autant plus que les substrats ultramafiques sont à l'origine de pseudo-karsts sujets à des affaissements localisés voire à des effondrements (Rouet 2009).

Par conséquent, on peut affirmer que la perte de couverture végétale entre le maquis ligno-herbacé et le maquis ligno-herbacé dégradé génère une augmentation de l'aléa érosion à l'échelle du bassin versant dont les conséquences ne se manifesteront pas nécessairement immédiatement. Cette

baisse du taux de couverture végétale entraînerait une baisse de la teneur en carbone organique du sol et de la Root Length Density, deux paramètres influençant la stabilité des agrégats du sol (Fig. 17), d'où la diminution significative de la stabilité des agrégats du sol entre le maquis ligno-herbacé et le maquis ligno-herbacé dégradé (Chapitre 3). En diminuant la couverture végétale, un seuil biotique (Hobbs and Harris 2001) entre les maquis ligno-herbacés dégradés et les maquis ligno-herbacés serait franchi. Les feux répétés seraient la cause principale du franchissement de ce seuil qui *in fine* limite le développement de la végétation (Jaffré *et al.* 1998).

Figure 20 – Exemple de ravine sur Ferralsols sur substrats ultramafiques

(photo : J. Demenois à la rivière des Pirogues)

Par ailleurs, la mise à nue, partielle ou totale, du sol serait propice à sa compaction, du moins superficielle, par effet « splash » provoqué par les gouttes de pluie. La teneur en eau du sol est le principal facteur influençant les processus de compaction (Soane and Van Ouwerkerk 1994). Une augmentation de la teneur en eau engendre une baisse de la pression au sol admissible (Medvedev and Cybulko 1995) et donc une augmentation de sa sensibilité à la compaction. Cette teneur en eau du sol va dépendre notamment de sa texture, particulièrement le pourcentage et le type d'argiles (Faure 1981), de la présence de matière organique, d'oxydes de fer et d'hydroxydes d'aluminium (Assouline *et al.* 1997). Aussi, la sensibilité à la compaction d'un sol est-elle un phénomène complexe et multifactoriel dont les causes sont largement méconnues pour ce qui est des Ferralsols sur substrats ultramafiques (Bourdon *et al.* 1994).

Bien que notre travail ne se soit pas précisément attaché à étudier ce phénomène de compaction, nous disposons d'un faisceau d'indices convergents dans ce sens. Tout d'abord, la masse volumique sèche du sol est significativement plus élevée (1,8 ± 0,2 g/cm^3) dans les maquis ligno-herbacés dégradés que dans les maquis ligno-herbacés (1,6 ± 0,2 g/cm^3). Or, la compaction entraîne une baisse des quantités d'air et d'eau contenues dans le sol, donc une augmentation de sa masse volumique (Hamza and Anderson 2005). Par ailleurs, l'analyse d'images 3D obtenues par micro-tomographie sur des agrégats de sol prélevés en maquis ligno-herbacé dégradé et en maquis ligno-herbacé (Fig. 21) semble révéler à la fois une moindre micro-porosité au sein des agrégats du sol du maquis ligno-herbacé dégradé et une organisation différente de celle-ci (« plan de cisaillement » *versus* « structure cylindrique »). Enfin, les sols de maquis ligno-herbacés dégradés se caractérisent par la présence de bactéries liées aux plus fortes teneurs en soufre échangeable (Gourmelon *et al.* 2016) qui pourrait indiquer l'existence de conditions anaérobiques propres aux sols compactés.

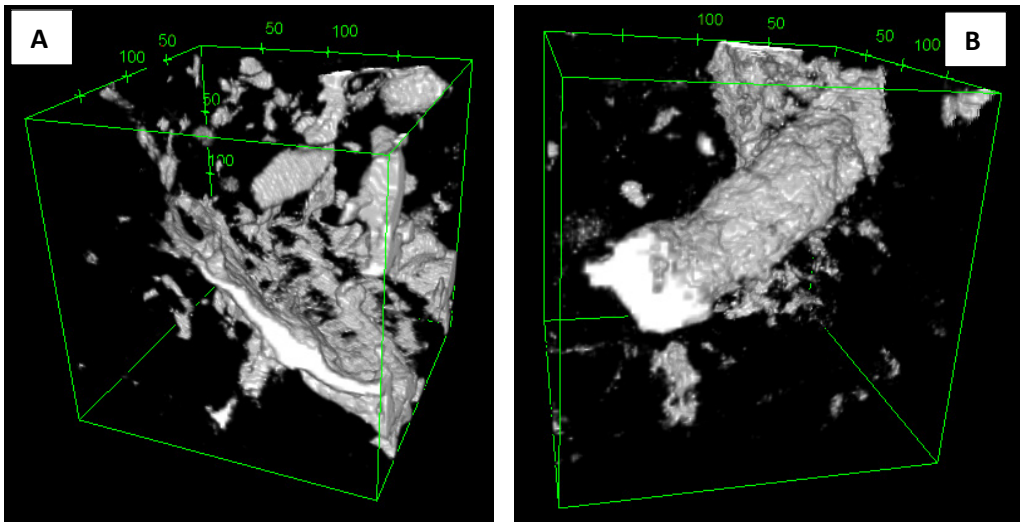

Figure 21 – Images 3D d'agrégats du sol obtenues par micro-tomographie

A : agrégat prélevé en maquis ligno-herbacé dégradé ; B : agrégat prélevé en maquis ligno-herbacé.
Les arêtes vertes correspondent à celles d'un cube de 1,4 mm de côté. La porosité y est représentée en blanc-gris. Les images ont été réalisées par le Laboratoire Navier – UMR 8205 (Ecole des Ponts Paris Tech – IFSTTAR – CNRS) et leur analyse menée avec l'appui méthodologique de l'UR Science du Sol de l'INRA.

Nous pensons que la compaction du sol constitue un seuil abiotique qui limite fortement l'installation et la croissance de la végétation dans les maquis ligno-herbacés dégradés. En effet, les effets négatifs de la compaction des sols sur la croissance des plantes ont été largement mis en évidence (Batey 2009; Harper *et al.* 1965; Kozlowski 1999) et limiteraient les possibilités de reconstituer un couvert végétal. Cette compaction rendrait la germination, la survie et la croissance des plantes d'autant plus difficile. Elle constituerait d'une part une barrière physique à la pénétration

de la radicelle dans le sol puis au développement des autres racines, et d'autre part elle altérerait la porosité des sols, et donc l'approvisionnement en eau et les échanges gazeux indispensables aux plantes. La sensibilité des plantes à la compaction du sol est toutefois variable selon les espèces (Hamza and Anderson 2005). Il nous semblerait donc intéressant d'étudier la capacité des plantes, d'une part à germer dans des conditions de forte compaction du sol, et d'autre part à croître dans de telles conditions. L'identification d'espèces végétales adaptées à ces conditions de compaction pourrait contribuer à sortir de ce mécanisme en « cercle vicieux » en s'appuyant sur de telles espèces-outils (Ghestem *et al.* 2014).

La combinaison de la diminution de la couverture végétale et de l'augmentation de la compaction du sol qui en résulte, limite, voire empêche, le développement de la végétation. Le passage répété des feux serait ainsi la cause principale du franchissement d'un seuil biotique (*e.g.* taux de couverture végétale) puis abiotique (*e.g.* compaction du sol) (Hobbs and Harris 2001) entre les maquis ligno-herbacés dégradés et les maquis ligno-herbacés, limitant la capacité de résilience des maquis ligno-herbacés dégradés. Ainsi, un mécanisme en « cercle vicieux » (Fig. 22) serait instauré, nécessitant des actions de restauration écologique pour le rompre et franchir ces seuils.

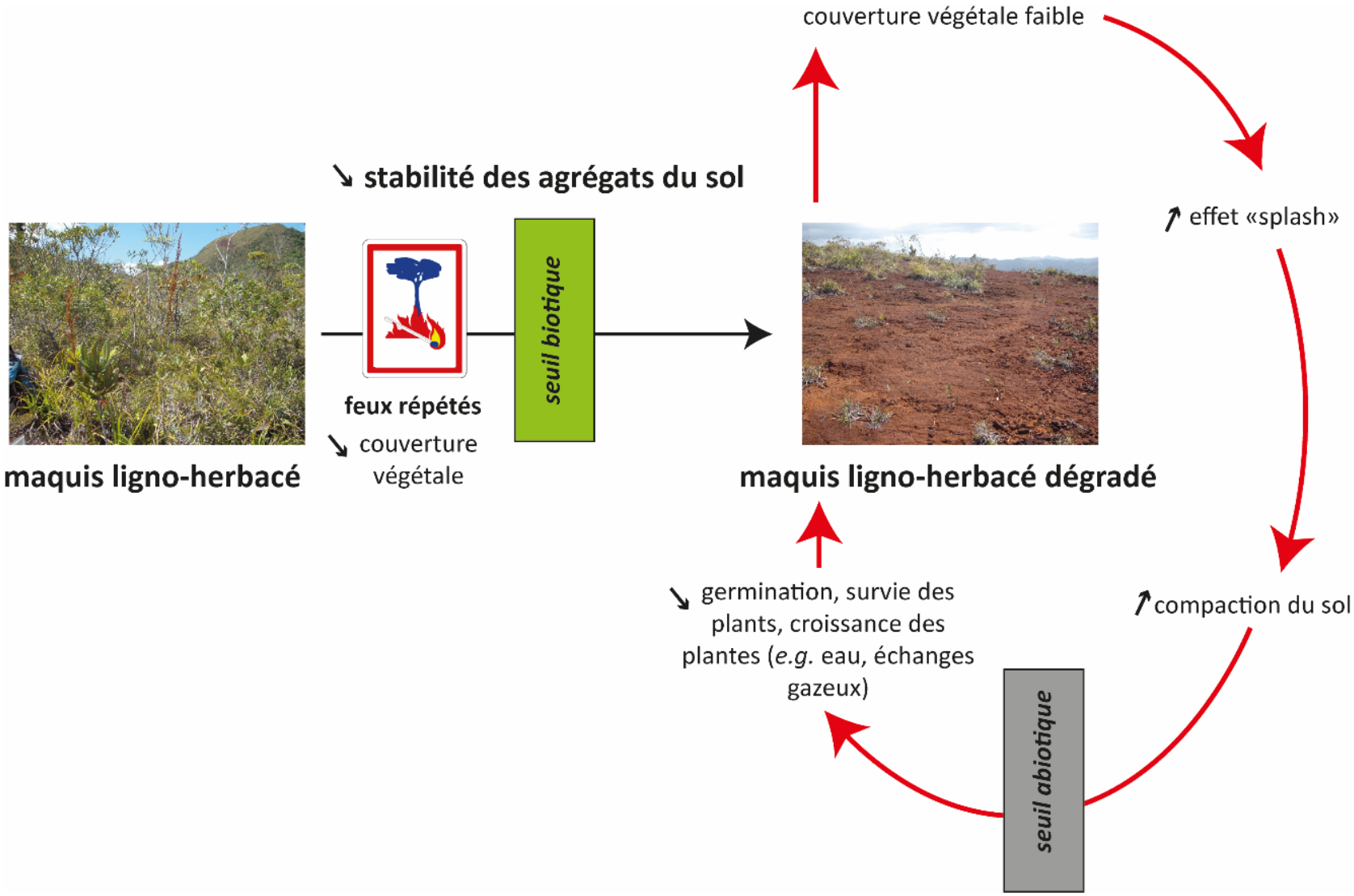

Figure 22 – Illustration du mécanisme en « cercle vicieux » et des seuils biotique et abiotique entre le maquis ligno-herbacé et le maquis ligno-herbacé dégradé par les passages répétés du feu

3. Quelles actions de restauration écologique pour limiter l'érosion hydrique des Ferralsols sur substrats ultramafiques ?

Comme nous venons de le voir, les actions de restauration écologique doivent se concentrer sur le passage d'un maquis ligno-herbacé dégradé à un maquis ligno-herbacé. Cela nécessiterait le passage d'un seuil abiotique (*e.g.* compaction du sol) puis d'un seuil biotique (*e.g.* taux de couverture végétale).

Remédier à la compaction du sol induit de parvenir à diminuer la densité apparente du sol. En milieu agricole, Hamza and Anderson (2005) suggèrent pour cela plusieurs techniques :

- ajouter de la matière organique dans le sol ;
- décompacter le sol à l'aide d'outils ;
- introduire une rotation avec des plantes disposant d'un système racinaire en pivot capable de pénétrer et de décompacter les sols.

Nous pouvons nous inspirer de ces savoir-faire dans le domaine de l'agriculture pour esquisser des pistes d'actions dans une optique de restauration écologique des maquis ligno-herbacés sur Ferralsols sur substrats ultramafiques.

Ainsi, la décompaction du sol pourrait être menée en intervenant selon la séquence suivante :

1. travailler superficiellement le sol afin de le décompacter. La forte stabilité des agrégats du sol, y compris en zone dénudée (Chapitres 3 et 4), constitue, de ce point de vue, un atout car elle doit permettre de limiter le risque d'érosion superficielle à la suite de ce travail de décompaction. Néanmoins, ce travail du sol devrait rester superficiel (< 10 cm), être réalisé selon les lignes de niveau pour éviter la création de griffes d'érosion du fait du ruissellement et être fait à l'aval d'obstacles physiques au ruissellement (*e.g.* zones végétalisées, blocs rocheux) ;
2. semer des espèces herbacées associées à des AMF afin de limiter, grâce à la création d'un premier couvert végétal, le risque de recompaction. Nous avons mis en évidence la capacité de *Costularia arundinacea* à augmenter la stabilité des agrégats du sol *via* ses racines et les mycorhizes associées, mais aussi à enrichir le sol en carbone organique. De manière plus générale, nous avons montré que toutes les espèces ne présentaient pas des valeurs de RLD équivalentes, traduisant une efficacité différente de leurs systèmes racinaires pour contribuer à limiter l'érosion hydrique (Chapitre 4). Nous avons également mis en évidence, en conditions contrôlées, que la mycorhization de *Costularia arundinacea* avec des AMF permettait d'accroître son efficacité et son efficience pour limiter la sensibilité du sol à l'érosion, *via* notamment une augmentation de la RLD. Il

conviendrait de poursuivre ce travail de caractérisation en ciblant en premier lieu les espèces connues pour être associées à des champignons. Dans l'état des connaissances actuelles, les espèces herbacées suivantes seraient ainsi concernées : *Costularia comosa, Costularia nervosa, Costularia pubescens, Schoenus neocaledonicus ;*

3. planter des espèces ligneuses associées à des ECM avec un système racinaire en pivot, afin de poursuivre la décompaction du sol en profondeur et d'augmenter sur le moyen et le long terme la teneur en matière organique du sol. D'après Martins and Angers (2015), les plantes de type-*B* (ligneuses) seraient en effet davantage aptes à favoriser la séquestration de carbone et d'accroître la quantité de matière organique au niveau des micro-agrégats. Nos travaux suggèrent que *Tristaniopsis glauca* et *Arillastrum gummiferum* pourraient être des espèces intéressantes dans cette optique (Chapitre 4).

Ces actions de décompaction, alliant intervention physique et ingénierie écologique, devraient ainsi permettre de franchir le seuil abiotique qui limite, voire empêche, l'augmentation du taux de couvert végétal qui constitue un deuxième seuil, biotique celui-ci.

Concernant le taux de couverture végétale, la question du taux minimal à atteindre afin de limiter efficacement l'aléa érosion est centrale. Les maquis ligno-herbacés dégradés étudiés présentent un taux de couverture végétale de 20 ± 6 % contre 80 ± 12 % pour les maquis ligno-herbacés à *T. glauca* (Chapitre 3). Sur cette base, on peut donc émettre l'hypothèse que le taux de couverture végétale minimum nécessaire pour limiter l'érosion hydrique pourrait se situer entre 25 et 70 %. Ces valeurs seraient cohérentes avec celles mentionnées par Vennetier *et al.* (2014). Ces auteurs soulignent qu'un recouvrement de 30 % réduit déjà significativement l'agressivité du ruissellement et parfois très fortement l'entraînement de particules. Par ailleurs, ils rappellent que les résultats expérimentaux montrent qu'un recouvrement de 70 % limite la mobilisation des particules de sols et les piège à proximité immédiate, presqu'aussi bien qu'un couvert complet. Si notre travail a permis de mettre en évidence l'existence d'un tel seuil de taux de recouvrement, la grande amplitude dans la valeur seuil (25 à 70 %) incite à développer des recherches le long d'une échelle de couvert végétal afin d'affiner cette valeur seuil.

Afin d'augmenter le taux de couverture végétale des maquis ligno-herbacés dégradés, nous proposons de s'appuyer sur leur hétérogénéité spatiale et la présence de micro-environnements (*e.g.* zone de dépôt de sédiments à l'aval de blocs de cuirasse) favorables à l'installation et au développement de la végétation. La prise en compte de ces micro-environnements s'avère en effet importante pour permettre l'installation de la végétation (Harper *et al.* 1965). Ainsi, les maquis ligno-

herbacés dégradés peuvent être comparés à une mosaïque composée de « tâches » de végétation essentiellement herbacées, dispersées au milieu de zones de sol nu et compacté et ponctuées de plantes isolées (Fig. 23).

Figure 23 – Illustrations de différents micro-environnements des maquis ligno-herbacés dégradés (photos : J. Demenois au Parc Provincial de la Rivière Bleue)

A : « tâche » de végétation essentiellement herbacée en aval d'un petit bloc rocheux entourée de latérite compactée ; B : plantes isolées au milieu d'une zone compactée

Les « tâches » de végétation correspondent aux zones à *C. arundinacea* étudiées en conditions *in situ* (Chapitre 4) et présentent une stabilité des agrégats plus importante, tout comme la teneur en carbone organique du sol ou en biomasse fongique. Les zones de sol nu et compacté seraient comparables aux conditions *in situ* rencontrées sous le témoin, *T. glauca* ou *A. gummiferum* (Chapitre 4). La stabilité des agrégats y est plus faible, en lien notamment avec la faible teneur en carbone organique. Ces « tâches » de végétation présentant moins de contraintes édaphiques (*e.g.* stabilité des agrégats plus élevées, teneur en SOC plus élevée, biomasse fongique plus abondante), la stratégie pour accroître le couvert végétal s'appuierait sur celles-ci afin d'augmenter leur superficie depuis leur lisière. Ainsi, l'augmentation du couvert végétal depuis les « tâches » de végétation pourrait être menée en enrichissant la végétation en espèces ligneuses en les plantant de façon privilégiée en lisière. Les « tâches » de végétation constitueraient des îlots de recolonisation et l'enjeu serait de rétablir une connectivité entre elles.

L'objectif serait multiple :

1. décompacter le sol à proximité de la « tâche » de végétation grâce à des espèces disposant d'un système racinaire en pivot ;
2. enrichir le sol en matière organique en utilisant des espèces végétales de type-*B* (*e.g.* riches en lignine) (Martins and Angers 2015) et ainsi améliorer les conditions édaphiques ;

3. limiter l'exposition du sol nu limitrophe à l'effet « splash » de la pluie grâce aux houppiers des espèces ligneuses (arbustives ou arborées), dont l'influence sur la couverture du sol irait au-delà de la superficie de la « tâche » de végétation ;
4. augmenter la résilience de la végétation au passage du feu *via* une plus grande diversité spécifique.

L'augmentation du couvert végétal pourrait conjointement se faire en valorisant les zones de dépôt de sédiments (*e.g.* aval de blocs de cuirasse) ou en en créant de nouvelles, en mettant en place de nouveaux obstacles au ruissellement (*e.g.* pierres, petits blocs rocheux) (Fig. 24), de préférence entre les « tâches » de végétation afin de réduire la vitesse de ruissellement de l'eau, et donc son pouvoir érosif. Nous pensons en effet que ces micro-environnements offrent un sol superficiellement plus meuble et relativement plus riche en éléments nutritifs du fait du lessivage en amont. Ils seraient de fait plus favorables à l'installation et au développement de la végétation. Dans ces zones, des espèces végétales aptes à survivre et croître dans des conditions édaphiques contraignantes (*e.g.* SLA, SRL élevées) pourraient être semées ou plantées en association avec des mycorhizes.

Figure 24 – Exemple de cordon rocheux mis en place sur zone compactée (photos : J. Demenois à la Coulée, aménagement DDR province Sud)

Les différentes étapes de ces actions de restauration écologique sont schématisées sur la figure 25. Elles doivent permettre de passer, sur un pas de temps à évaluer mais *a priori* long (Perry and Enright 2002 ; Mc Coy et *al.* 1999), d'un taux de couverture végétale d'environ 5 % avant

restauration à un couvert végétal objectif de l'ordre de 70 % présentant une plus grande diversité spécifique, afin de conférer une plus grande résilience au feu et contribuer à accroître la stabilité des agrégats du sol (Erktan *et al.* 2016).

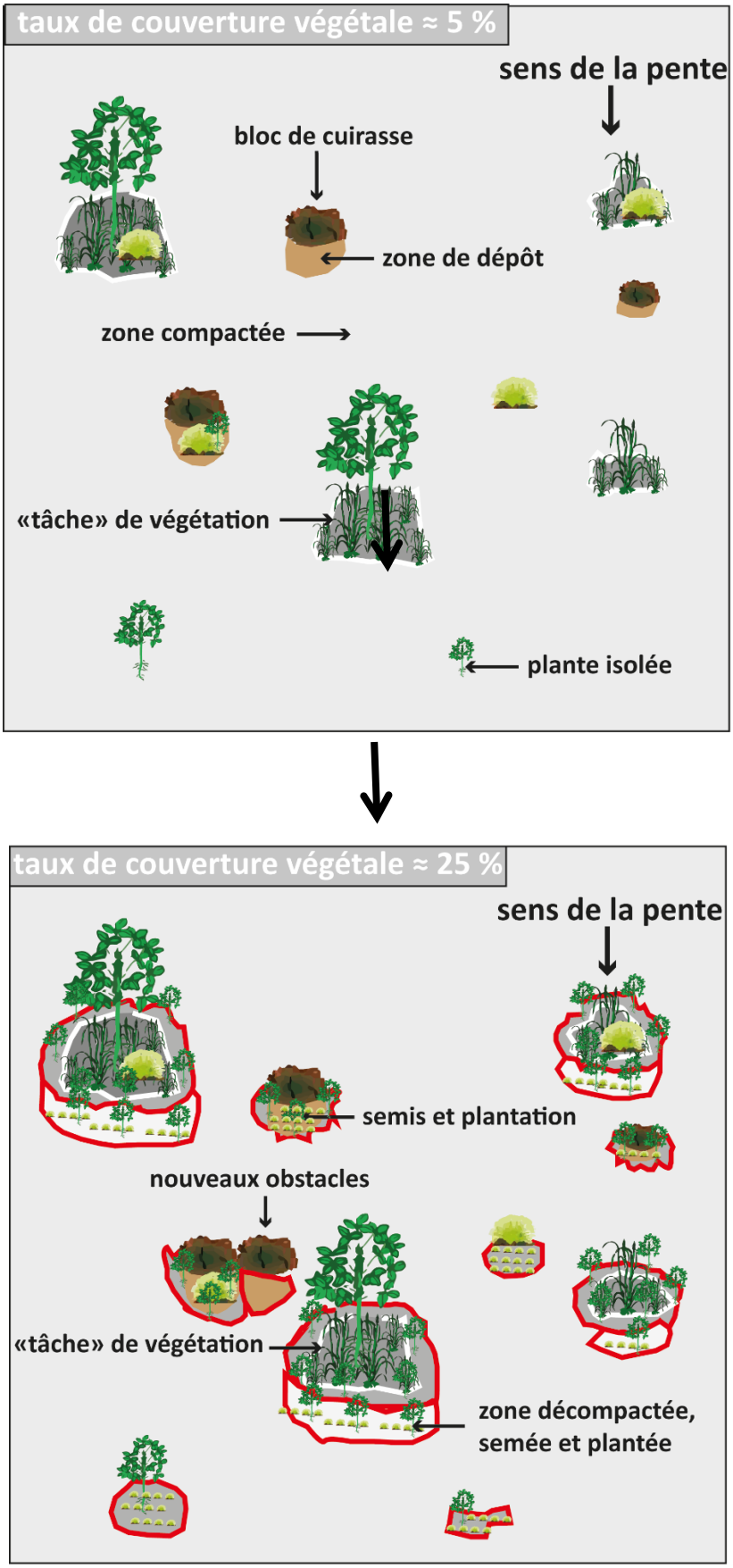

Figure 25 – Schéma des actions de restauration écologique des maquis ligno-herbacées dégradés sur Ferralsols sur substrats ultramafiques

Ces différentes actions de restauration écologique peuvent se résumer par les préconisations suivantes :

- prendre en compte la sensibilité à la compaction des Ferralsols sur substrats ultramafiques ;
- prendre en compte les micro-environnements du milieu à restaurer ;
- revégétaliser en « tâches » pour obtenir une Root Length Density élevée et augmenter la teneur en carbone organique du sol, donc la stabilité des agrégats du sol ;
- introduire des espèces ligneuses mycorhizées avec des herbacées mycorhizées pour décompacter en profondeur les sols et augmenter sur la durée la teneur en carbone organique du sol, donc la stabilité des agrégats du sol ;
- viser un taux de couverture végétale de 70 % pour réduire efficacement l'aléa érosion et rétablir les fonctionnalités des maquis ligno-herbacés dégradés.

4. Quelles perspectives de recherche ?

Une telle stratégie de restauration écologique nécessiterait de développer des actions de recherche afin de répondre notamment aux questions suivantes :

- quels sont les paramètres influençant la sensibilité à la compaction des Ferralsols sur substrats ultramafiques ? Une meilleure compréhension du phénomène permettrait de mieux appréhender leur décompaction ;
- quelles espèces végétales sont aptes à germer dans des conditions de forte compaction du sol et quels sont leurs traits fonctionnels ? L'objectif serait de caractériser et identifier des espèces-outils pour recoloniser les Ferralsols compactés ;
- quelles espèces végétales sont aptes à décompacter les Ferralsols et quels sont leurs traits fonctionnels ? L'objectif serait de caractériser et identifier des espèces-outils pour décompacter les Ferralsols ;
- quel seuil de couvert végétal permet de restaurer les fonctionnalités d'un maquis ligno-herbacé dégradé ? Un seuil se situant entre 25 et 70 % est mis en évidence par nos travaux mais celui-ci devrait être affiné. Cela nécessiterait par exemple de développer une approche similaire à la nôtre le long d'un gradient de couvert végétal ;
- comment les micro-environnements liés à l'hétérogénéité spatiale de la couverture du sol influencent l'installation et le développement de la végétation ? La prise en compte de ces micro-environnements s'avère en effet importante pour permettre l'installation progressive de la végétation dans les maquis ligno-herbacés dégradés ;
- quelle est l'influence de la diversité spécifique (végétale, fongique, bactérienne) sur les fonctionnalités des maquis ligno-herbacés ? L'augmentation de la diversité spécifique devrait conférer une plus grande résilience des maquis restaurés ;
- quels sont les bilans hydriques sur Ferralsols sur substrats ultramafiques ? De tels bilans permettraient de mieux comprendre l'influence des formations végétales sur l'érosion hydrique à l'échelle du bassin versant.

5. Le mot de la fin

Le chantier de la restauration écologique des Ferralsols sur substrats ultramafiques est vaste. Nos travaux permettent, à leur échelle, de l'éclairer sous un autre angle, en s'intéressant à sa face cachée (sol, racines et micro-organismes du sol). Il n'en demeure pas moins que le maintien des services écosystémiques liés aux écosystèmes forestiers passe avant tout par la préservation de ces derniers, leur restauration relevant d'une forme d'idéal. Les efforts menés pour développer des techniques de restauration écologique ne nous confèrent pas un droit à dégrader les milieux naturels mais au contraire nous obligent à faire preuve d'encore davantage d'humilité et de respect face à la complexité du vivant.

« *Un tiens vaut mieux que deux tu l'auras* » (Jean de La Fontaine).

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Title : Influence of mycorrhizal symbiosis and root traits on the erosion of tropical soils? Application to the ecological restoration of degraded forest ecosystems of New Caledonia on Ferralsols developed on ultramafic substrates

Keywords : soil aggregate stability ; ultramafic substrates ; root traits ; mycorrhiza ; ecological restoration ; New Caledonia

Abstract :

Tropical forest ecosystems cover nearly half of the world's forest area. These ecosystems provide basic services for the well-being of our societies (e.g. regulation of material flows, soil preservation) are particularly affected (loss and degradation of forests) by global changes. New Caledonia, and its ultramafic substrates, is no exception to this trend. Mining and fires are responsible for forest regression, fragmentation, degradation and soil erosion. The archipelago is ranked among the hotspots of global biodiversity and the ecological restoration of these ecosystems is a major challenge.

The objective of this thesis is to contribute to the ecological restoration of the forests of New Caledonia in order to limit the erosion of soils on ultramafic substrates and is part of the disciplinary field of the ecology of restoration. The scientific objective is to study the influence of mycorrhizal symbiosis and root traits on the erosion of Ferralsols developed on ultramafic substrates through a multi-scale approach.

In the first part, we highlight the floristic and structural characteristics of plant communities on ultramafic substrates. These suggest an increased expression of the root traits of dominant species in monodominant forests. The central place of fire and cyclones in the dynamics of plant succession is also emphasized, as well as mycorrhizal symbioses in maintaining the monodominance of *Nothofagus aequilateralis*.

In the second part, our work suggests the existence of a biotic threshold between degraded ligno-herbaceous maquis and ligno-herbaceous maquis. Repeated fires would be the main cause of crossing this threshold. The increase in plant biomass would be the key factor contributing to the stability of the aggregates between these two stages. Thus, fire protection combined with the promotion of plant successions through the use of potentially facilitating species such as *Costularia arundinacea* could be an efficient strategy for limiting erosion of Ferralsols. In addition, the influence of plant (*e.g.* floristic composition) and fungal communities (*e.g.* biomass) on the stability of aggregates is clearly highlighted.

The third part aims to evaluate the ability of plant species, combined with mycorrhizal fungi, to increase the stability of aggregates, but also to identify root traits and mycorrhizal associations contributing to this increase. In this section, we demonstrate that the combination of high values for “Root Mass Density - Root Length Density – percentage of fine roots” is effective in increasing aggregate stability. Moreover, the efficacy of this combination of root traits is enhanced by mycorrhizal symbiosis. Thus, of the three plant species evaluated, *Costularia arundinacea* would be the most effective tool species for increasing the stability of aggregates.

This work allowed us to highlight the influence of root traits and mycorrhizal symbiosis on the stability of soil aggregates on Ferralsols on ultramafic substrates, at the scale of plant communities or at the level of plant species. To our knowledge, these results are the first to be acquired on this type of soil. These results make it possible to formulate proposals for the ecological restoration of forest ecosystems in New Caledonia in order to limit soil erosion on ultramafic substrates, but also to sketch new avenues of research.

Titre : Quelle influence des symbioses mycorhiziennes et des traits racinaires sur l'érosion des sols tropicaux ? Application à la restauration écologique des écosystèmes forestiers dégradés de Nouvelle-Calédonie sur Ferralsols développés sur substrats ultramafiques

Mots clés : stabilité des agrégats du sol ; substrats ultramafiques ; traits racinaires ; mycorhizes ; restauration écologique ; Nouvelle-Calédonie.

Résumé :

Les écosystèmes forestiers tropicaux représentent près de la moitié de la superficie forestière mondiale. Ces écosystèmes qui fournissent des services fondamentaux pour le bien-être de nos sociétés (*e.g.* régulation des flux de matières, maintien des sols) sont particulièrement touchés (perte et dégradation des forêts) par les changements globaux. La Nouvelle-Calédonie, et ses substrats ultramafiques, ne font pas exception à cette tendance. L'activité minière et les feux sont responsables de la régression, de la fragmentation, de la dégradation des forêts et de l'érosion des sols. L'archipel est classé parmi les points chauds de la biodiversité mondiale et la restauration écologique de ces écosystèmes revêt de forts enjeux.

L'objectif appliqué de cette thèse est de contribuer à la restauration écologique des forêts de Nouvelle-Calédonie afin de limiter l'érosion des sols sur substrats ultramafiques, et s'inscrit dans le champ disciplinaire de l'écologie de la restauration. L'objectif scientifique est d'étudier l'influence des symbioses mycorhiziennes et des traits racinaires sur l'érosion des Ferralsols développés sur substrats ultramafiques à travers une approche multi-échelle.

Dans la première partie, nous mettons en évidence les caractéristiques floristiques et structurales de communautés végétales sur substrats ultramafiques. Celles-ci laissent présager une expression accrue des traits racinaires des espèces dominantes dans les forêts monodominantes. La place centrale du feu et des cyclones dans la dynamique de succession végétale est également soulignée, tout comme celle des symbioses mycorhiziennes dans le maintien de la monodominance de *Nothofagus aequilateralis*.

Dans la deuxième partie, notre travail permet de suggérer l'existence d'un seuil biotique entre les maquis ligno-herbacés dégradés et les maquis ligno-herbacés. Les feux répétés seraient la cause principale du franchissement de ce seuil. L'augmentation de la biomasse végétale constituerait en effet le facteur-clé contribuant à accroître la stabilité des agrégats entre ces deux stades. Ainsi, la protection contre les feux, associée à la promotion des successions végétales à travers l'utilisation d'espèces potentiellement facilitatrices comme *Costularia arundinacea* pourrait constituer une stratégie efficiente pour limiter l'érosion des Ferralsols. De plus, l'influence des communautés végétales (*e.g.* composition floristique) et fongiques (*e.g.* biomasse) sur la stabilité des agrégats est clairement mise en exergue.

La troisième partie vise à évaluer la capacité d'espèces végétales, associées à des champignons mycorhiziens, à accroître la stabilité des agrégats, mais aussi à identifier les traits racinaires et les associations mycorhiziennes contribuant à cet accroissement. Dans cette partie, nous mettons en évidence que la combinaison de valeurs élevées des traits racinaires « Root Mass Density – Root Length Density – pourcentage de racines fines » est efficace pour augmenter la stabilité des agrégats. Par ailleurs, l'efficacité de cette combinaison de traits racinaires est accrue par les symbioses mycorhiziennes. Ainsi, des trois espèces végétales évaluées, *Costularia arundinacea* serait l'espèce-outil la plus efficace pour accroître la stabilité des agrégats.

Ce travail a ainsi permis de mettre en évidence l'influence des traits racinaires et des symbioses mycorhiziennes sur la stabilité des agrégats des Ferralsols sur substrats ultramafiques, que ce soit à l'échelle des espèces ou des communautés végétales. A notre connaissance, ces résultats sont les premiers acquis sur ce type de sol. Ces résultats permettent de formuler des propositions en vue de la restauration écologique des milieux forestiers de Nouvelle-Calédonie afin de limiter l'érosion des sols sur substrats ultramafiques, mais aussi d'esquisser de nouvelles pistes de recherche.